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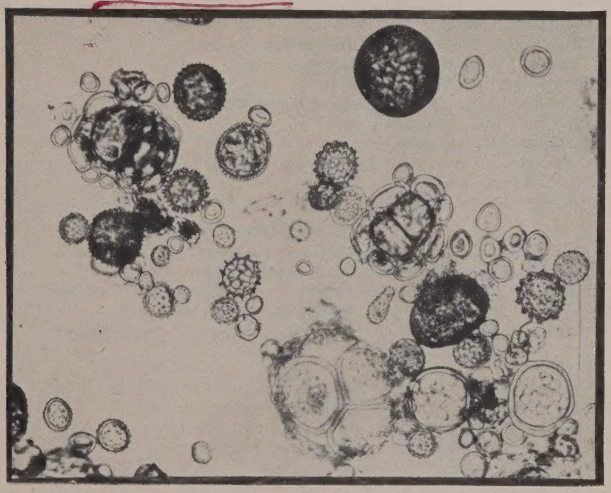
The Ustilaginales or "Smuts" of Washington

By
George W. Fischer and Elisa Hirschhorn



Seventeen species of Washington's smuts, as they appear under the microscope. Magnified about 600 diameters.

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The Ustilaginales or "Smuts" of Washington

George W. Fischer and Elisa Hirschhorn[1]

INTRODUCTION

Approximately one-fifth of the smuts reported for the entire North American Continent are known to occur in the State of Washington. It is thus readily apparent that this important group of plant parasites is well represented in this State. One hundred and forty-six species of plants serve as hosts to the smut-fungi reported for Washington State. Considerable interest has been manifested in the nature and identity of the numerous smuts occurring in Washington and adjacent territory. The primary purpose of the present work is to provide an illustrated manual for the use of plant pathologists, agronomists, mycologists, teachers, students, county agents, and other interested persons in the State of Washington, and in neighboring States.

The "USTILAGINALES OF WASHINGTON" has been prepared with the view of being practically useful. The usual presentation of species is on a basis of supposed phylogenetic sequence, grouping all species of a genus together in one section which is preceded by a description of the general characters of the genus. This orthodox presentation is not deemed expedient for the purposes of this manual. Prosaic descriptions of the families and genera of smuts are adequately abundant in the strictly taxonomic works that have appeared during the past half-century and references to these works are given in the Bibliography. In the USTILAGINALES OR "SMUTS" OF WASHINGTON the species are grouped together primarily on the basis of symptoms, and the keys are similarly constructed. Thus, the smut-fungi of Washington are divided into four sections: Stem Smuts, Leaf Smuts, Inflorescence Smuts, and Gall-forming Smuts. These groups are very distinct and the student can, in the great majority of cases, readily determine in which group to look for a given smut.

The concept of species as embodied in the present work will probably be at variance with old long-established concepts in many instances. The present day tendency is away from the physiologic concept and back to the orginal, or Linnaeen, concept based strictly on the morphology or structure of the organism. Following this concept, it will be noted that, for example, the loose smut of wheat and the loose smut of barley are considered as members of one morphologic species. They are indistinguishable in their structure, life history,

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control, and effect upon the host plant. They differ only in the specialization of one to barley and the other to wheat varieties. If species were to continue to be recognized on such a purely physiologic basis there could result a species name for every physiologic variant,—which would be a confusing chaotic multiplicity of "species" beyond the comprehension of even the most specialized smutologist. Similarly, the covered smut of oats and the covered smut of barley are herein considered as one morphologic species; also the loose smut of oats, the loose smut of tall oatgrass, and the black loose smut of barley. Conformity to the International Rules of Botanical Nomenclature requires that the oldest available specific name shall apply. Unfortunately, this sometimes results in a name not logically applicable to a composite species. Thus, *Ustilago avenae* must be taken for the species name to designate the morphologic species including the loose smut of oats, the loose smut of tall oatgrass, and the black loose smut of barley; these smuts have earlier had their own names: *U. avenae, U. perennans,* and *U. nigra* respectively. The latter name would be preferable for the combined species because it indicates black sori, but *avenae* is the oldest name available and must be used in spite of the fact that it implies specialization to *Avena,* or oats.

We gratefully acknowledge the invaluable assistance rendered in the loan of herbarium material for critical examination during the preparation of this bulletin. Especially helpful and cooperative have been Mr. John A. Stevenson, Senior Mycologist in Charge, Mycological Collections, Bureau of Plant Industry, Soils, and Agricultural Engineering, United States Department of Agriculture, and Dr. David H. Linder, Curator, Farlow Herbarium of Cryptogamic Botany, Harvard University.

The Nature of the Smuts

The common name "smut" has it derivation from words meaning to besmirch or to smudge. The application of the name in this sense refers of course to the more common aspects of the smuts,—the presence of localized sooty, black or brownish masses on the affected plants. All the smuts are plant parasites, and some are of well-known economic importance, preying on important cereal, grass, and vegetable crops. Familiar examples of such destructive smuts are bunt or stinking smut of wheat, oat smuts, barley smuts, corn smut, stripe smut of grasses, and onion smut, and the extensive losses which smuts sustain is common knowledge. Actually, the name smut is used to designate the disease, as well as the organism responsible. However, the latter is more correctly spoken of as the "smut-fungus."

The familiar brownish or black smut-mass is called the *sorus* (plural, *sori*) and is composed chiefly of many thousands of tiny, microscopic bodies called *spores.* These spores are the "seeds" of the smut fungus, and serve, therefore, for reproduction and resistance to un-

favorable environment. Smut spores present a rather wide variety of forms (see cover page), with reference to size, color, markings, etc. The unit of measurement is usually the micron (signified by the Greek letter mu, μ) which is approximately 1/25,000 inch. The smallest smut spores are about 3.5-4μ in diameter, and the largest about 35-40μ. The spore wall may be perfectly smooth or variously adorned with dots, spines, warts, or reticulations. Terms used to describe the nature of the exterior surface of the spore wall are as follows:

Smooth	no markings, indentations of any kind
Pitted	provided with minute circular pits
Punctate	provided with dots
Echinulate	provided with spines or pointed protuberances
Verrucose	provided with wart-like protuberances
Reticulate	provided with polygonal meshes or depressions
Cerebriform	reticulations becoming very irregular, so as to resemble brain-like convolutions.

The size and wall markings of the spores are very important diagnostic characters.

Most of the smuts are restricted in the localization of their sori in the host plants. Some produce their spores only in the ovaries, without affecting any of the surrounding floral parts. Other smuts sporulate in the leaves, or in the ovules, etc. Some smuts destroy the entire inflorescence (floral structure); others are restricted to the anthers only. One group of smuts is almost entirely confined to the stems of grasses; other smuts produce galls or tumor-like structures on various parts of the host plants, as in the case of the common smut of corn.

Germinating smut spores usually produce a hyaline (colorless) tube with 2-4 cross walls. This tube is called the *promycelium*. From the cells of this structure tiny ovoid or elliptical yeast-like cells are frequently borne. These are the *sporidia*. Some smuts do not produce sporidia, but only a much-branched system of microscopic fungus tubes, called a *mycelium*. Other smuts bear sporidia on the mycelium. Infection of the host plant usually takes place when the spore germinates. In the case of many cereal and grass smuts this infection takes place in the seedlings since both the seeds and the smut spores germinate at about the same time. The germinating spore sends forth an infection tube which penetrates the epidermis of the seedling and initiates an internal mycelium. This mycelium grows and develops within the growing and developing plant, usually giving no evidence of infection until smut spores are produced, in the leaves, ovaries, stamens, inflorescence, or wherever the genetic nature of the smut-fungus dictates. Familiar examples of seedling-infecting smuts are bunt or stinking smut of wheat, covered smut of barley, oat smuts, and stripe smut and head smut of grasses. It is now well-known that such smuts can be controlled by treating the seeds with a fungicidal dust

that kills the smut spores either before or during germination but has no harmful effect on the seeds themselves.

Although the vast majority of smut-fungi can produce spores only in the tissues of their respective host plants, it is well-known that they can develop a mycelium, or sporidia, or both in the soil, decaying refuse, nutrient solutions, or solid media.

Many smut fungi exhibit a remarkable degree of specialization, not only to certain species of plants, but also to certain varieties or strains within species. Similarly, there are often strains or "races" of the smut fungus with which to contend. Thus, in the common stinking smut of wheat for example, there are many known strains or "races", each capable of attacking different varieties of wheat. The control of smut diseases through the use of resistant varieties is therefore a battle of smut varieties versus plant varieties, the former being directed by Nature and the latter by man with the help of Nature.

The Technique of Identifying Smuts

The process of identification of smuts is largely based on microscopic characters. A good microscope is, therefore, the first prerequisite. Since species determination often depends on the detection of minute spots, warts, reticulations, etc. on the spore wall, a magnification of 900 diameters is frequently necessary, although 400 diameters is usually sufficient for the larger-spored species. Nevertheless, it is strongly recommended that the spores be examined under oil-immersion objective, otherwise positive identification may be impossible.

Since the size of spores is an important diagnostic character it is necessary that the microscope be provided with an ocular micrometer, the divisions of which have been accurately calibrated.

It is a good practice in the study of dry specimens or herbarium material, to mount the spores in a drop of lacto-phenol.[1] After the cover slip has been put in place the mount should be heated over a small flame or on a small electric hot plate to the bubbling point, i.e. just under boiling. The hot lacto-phenol expands the shrunken dry spores to their normal, "fresh" size.

It is important in the microscopic examination of the spores of a smut collection to study a truly representative sample of the spores. The mount should be given a good general survey, noting the general characters of the spores: color, markings, shape, extremes in size, etc. Then, 25-30 spores should be measured (more if there is much variation) to determine the range in spore dimensions. With these microscopic data and with the specimens at hand, the student is ready to begin to "identify" the smut.

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[1] Lacto-phenol:
20 c.c glycerine
20 c.c. lactic acid
20 grams phenol
20 cc. water

There are two methods commonly employed in identifying smuts. One, the "orthodox" method, involves the use of a key to "run down" an unknown. The other method is the host-index method, in which the user looks in the index to see what smuts have been reported on the host plant of his unknown smut and then proceeds to study the descriptions and illustrations of the smuts on that host until he finally finds the species description which corresponds to the unknown.

The key method is really the better, more reliable method in many instances, although time is often saved by referring to the host-index. A disadvantage in the host-index method arises when one is attempting to identify a smut that happens to be on a new host plant. In this case, the student may find that no smut has been described on the particular host plant in case. Or he may find 4 or 5 smuts listed for that host, and subsequently discover that the unknown smut at hand is different from all of them. Obviously, in instances like these the use of the key would save time. Finally, the use of the key is strongly recommended to the student because it necessitates a thorough study of the smut to be identified, thereby serving to further educate the student in the morphology of the smuts.

The key, which follows, is primarily a dichotomous key, i.e. it requires a decision on one of two alternatives, before proceeding further. In a few places, however, it has been found expedient to provide 3 or 4 alternatives.

KEY TO THE USTILAGINALES OR "SMUTS" OF WASHINGTON

Sori primarily in the stems, surrounding the internodes of grasses .....Part 1. Stem Smuts

Soris primarily in the leaves, as stripes, spots, pustules or marginal areas .....Part 2. Leaf Smuts

Sori primarily in various parts of the inflorescence .....Part 3. Inflorescence Smuts

Sori forming conspicuous galls, nodules, tumors, etc. on various parts of the host .....Part 4. Gall-forming Smuts

Part 1. Stem Smuts

Spores with bipolar areas (oil immersion) evident as:

Bipolar areas varying from entire apical thickenings of the wall to minutely echinulate or dentate areas; spores mostly 5-7μ in diameter ..... 3. *Ustilago spegazzinii*

Bipolar areas consisting of cap-like appendages, or these may be evident as deep cracks in the exospore; spores mostly 7-10μ in diameter ..... 4. *Ustilago williamsii*

Spores without any evidence of bipolar areas.

Sori at first covered by delicate membrane, host *Distichlis* ..... 2. *Ustilago halophila*

Sori entirely naked, except for enveloping leaf sheath, host *Stipa* and *Oryzopsis* ..... 1. *Ustilago nummularia*

Part 2. Leaf Smuts

Sori evident as long and short stripes, chiefly in leaves and leaf sheaths often resulting in a shredded appearance; on grasses and cereals.

Sori brown, spores 3.5-8μ in diameter.

Spores mostly 4 x 5μ, not on *Glyceria* ..... 20. *Ustilago sitanii*

Spores mostly 4-7 x 7-9μ, on *Glyceria* ..... 5. *Ustilago longissima*

Sori black, spores larger

Spores in "balls" of 1-4, invested by a layer of smaller, hyaline to pale-brown sterile cells ..... 10. *Urocystis agropyri*

Spores free, not in balls

Spores chiefly 9-12μ in diameter, echinulate ..... 6. *Ustilago striiformis*

Spores chiefly 14-18μ in diameter, verrucose or coarsely echinulate.

Spores mostly coarsely verrucose; on *Agropyron* and *Elymus* ..... 7. *Ustilago aculeata.*

Spores mostly coarsely echinulate; on *Phalaris* ..... 8. *Ustilago echinata*

Sori not evident as long and short stripes

Sori chiefly marginal, spores densely echinulate, 11-15μ, on *Polygonum* ..... 9. *Ustilago bistortarum*

Sori chiefly forming scattered spots or irregular areas; hosts other than *Polygonum.*

Spores more or less in true "balls" of 2-30 or more

Spore-balls 100-200μ in diameter.

Spores 8-10μ in diameter, host *Alisma* ..... 17. *Doassansia alismatis*

Spores 10-15μ in diameter, host *Potamogeton* ..... 18. *Doassansia martianoffiana*

Spore-balls less than 100μ in diameter, usually not over 60μ

Spore-balls consisting of 8-30 spores, firmly united. ..... 15. *Tuburcinia trientalis*

Spore-balls consisting of 2-4 spores (occasionally more), rather easily separated ..... 16. *Whetzelia waldsteiniae*

Spores not in true balls, but tending to adhere together in irregular, asymmetrical groups; spores embedded in host tissues, usually pale, globose (irregular in shape, and darker in *Entyloma irregulare*)

Spores olivaceous-brown, very irregular in shape; on grasses ....11. *Entyloma irregulare*

Spores pale yellowish to pale yellowish-brown mostly globose or subglobose; not on grasses.

Spores often with hyaline envelope

Envelope irregularly thick, resulting in more or less tuberculate projections, on *Arnica* spp. ....13. *Entlyoma arnicale*

Envelope rather uniformly thin; on *Ranunculus* spp..... .....12. *Entyloma ranunculi*

Spores lacking hyaline envelope; on *Compositae* ....14. *Entyloma compositarium*

Part 3. Inflorescence Smuts

Sori in the ovaries only, not involving supporting floral structures

Spores perfectly smooth, large (17-20μ in diameter), host *Triticum* .....44. *Tilletia foetida*

Spores (under oil immersion, 500 x or more) not perfectly smooth.

Spores more or less reticulate (oil immersion), reticulations sometimes appearing irregular or cerebriform.

Spores 7-12μ in diameter.

Spores hyaline to pale violaceous, reticulations about 1μ in diameter .....39. *Ustilago vinosa.*

Spores deep violaceous, reticulations 2-4μ in diameter, prominent .....29. *Ustilago utriculosa*

Spores 13-28μ in diameter

Sori naked, straw-yellow, on *Luzula* ....37. *Ustilago vuijckii.*

Sori enclosed by ovary wall, on cereals and grasses

Spores 15-23μ in diameter.

Spores enveloped by thin hyaline membrane; sterile cells laminated, 21-28μ ....50. *Tilletia asperfolia*

Spores without membrane; sterile cells thin-walled, 12-18μ .....45. *Tilletia caries.*

Spores 21-28μ in diameter

Spore-mass light chestnut brown, on *Bromus* spp. ....46. *Tilletia guyotiana*

Spore-mass dark reddish-brown to brownish black....

Sterile cells 12-17μ; on *Deschampsia* spp. ..... 51. *Tilletia cerebrina*

Sterile cells larger, chiefly 15-21μ

On *Elymus* .....49. *Tilletia elymi*

On *Holcus* .....48. *Tilletia holci*

On *Festuca* .....47. *Tilletia fusca*

Spores punctate, echinulate, verrucose, etc. but not reticulate

Spore-mass dark purplish ..... 31. *Sphacelotheca hydropiperis*

Spore-mass olive-brown to almost black.

Hosts: *Carex* spp.

Spores punctate, 16-21μ ..... 27. *Cintractia caricis*

Spores verrucose, 5-8 x 7-14μ ..... 28. *Farysia olivacea*

Hosts: Grasses

Spores 9-11μ, angular; on *Aristida* spp. ..... 35. *Sorosporium consanguineum*

Spores 5-7μ, globose; on *Sorghum* spp. ..... 36. *Sphacelotheca sorghi*

Spores 10-14μ, distinctly echinulate; on *Setaria* spp. ..... 22. *Ustilago neglecta*

Sori not confined to the ovaries; in various parts of the inflorescence, including or not including the ovaries.

Sori often entirely consuming the inflorescence, including the rachis.

Spores mostly less than 12μ in diameter.

Spores mostly 4-5μ in diameter, finely echinulate ..... 20. *Ustilago sitanii*

Spores 5-8μ in diameter, prominently granular-verrucose, on *Danthonia* spp. .....21. *Ustilago residua*

Spores larger, punctate to finely echinulate.

Spores 7-10μ, more or less punctate (oil immersion); on *Panicum miliaceum* .....32. *Sphacelotheca destruens*

Spores 9-12μ, abundantly and minutely echinulate; on *Zea mays* and *Sorghum* spp. 33. *Sphacelotheca reiliana*

Spores 8-11μ, minutely verrucose, spore-balls usually present; on *Panicum* spp.....34. *Sorosporium syntherismae*

Spores mostly more than 12μ in diameter

Spores dark reddish-brown, opaque, verrucose; on *Festuca* spp. .....23. *Ustilago mulfordiana*

Spores purplish, deeply pitted, on *Polygonum* spp. ..... 30. *Ustilago punctata*

Sori involving the ovules only

Spores firmly united into definite spore-balls, coarsely verrucose, on *Leguminosae* .....42. *Thecaphora deformans*

Spores entirely free

Spores 10-14μ in diameter, minutely reticulate; on *Caryophyllaceae* .....38. *Ustilago alsineae*

Spores 14-18μ in diameter, distinctly reticulate; on *Claytonia* .....41. *Ustilago claytoniae*

Sori in the anthers only; on *Caryophyllaceae* .....40. *Ustilago violacea*

Sori involving the ovaries and also more or less the enveloping structures; on *Gramineae* and *Cyperaceae.*

Spores firmly united in balls; on *Carex* .....43. *Thecaphora aterrima*

Spores entirely free; on *Gramineae*

Spores smooth .....26. *Ustilago hordei*

Spores minutely echinulate to verrucose

Spores mostly 5-8μ in diameter, minutely echinulate, often lighter colored on one side

Sori forming striae in uppermost leaves and sheaths as well as in the aborted inflorescence, spore-mass light brown .....20. *Ustilago sitanii*

Sori usually in spikelets only, often involving all but the rachis of the inflorescence; spore-mass dark olive-brown to almost black

Spores when germinating producing mycelium only, no sporidia .....19. *Ustilago nuda*

Spores in germination producing a promycelium with sporidia (especially on nutrient media) .....24. *Ustilago avenae*

Spores mostly 7-12μ in diameter, minutely echinulate to (more often) distinctly granular-verrucose, not lighter-colored on one side .....25. *Ustilago bullata*

Part 4. Gall-forming Smuts

Sori covered at first by a tough, hispid membrane; spores mostly 10-14μ in diameter; on *Echinocholoa* .....53. *Ustilago crus-galli*

Sori covered at first by a smooth, whitish, rather fragile membrane; spores mostly 9-12μ in diameter; on *Zea mays* .....52. *Ustilago maydis.*

PART ONE

STEM SMUTS

1. USTILAGO NUMMULARIA Speg. An. Mus. Nac. de Buenos Aires, ser. 3, 1:59. 1902.

Sori surrounding the internodes and sometimes extending into the more or less aborted inflorescence, enclosed at first by the leaf sheaths, dusty, dark-brown to almost black; spores globose to subglobose, yellowish, brown, or olivaceous, smooth, chiefly 4-5μ in in diameter, or 3-4 x 5-5μ. Fig. 1.

On Gramineae:

Oryzopsis hymenoides (Roem. and Schult.) Ricker. Washington, Oregon, Idaho.

Stipa comata Trin. and Rupr. Washington, Oregon, Idaho.

Germination has been observed on malt extract-dextrose agar at room temperature (18-19° C). After about 48-60 hrs. a slender, hyaline germ tube emerges which develops rather rapidly, with sparse branching. Often the promycelium becomes 4-celled and from each cell a branch protrudes as though primary sporidia were in the process of development in the classic fashion of sporidia-producing smuts, but these protuberances merely develop into branches.

Plants of *Stipa* and *Oryzopis* infected with *Ustilago nummularia* have a characteristic appearance. When the affected culms are young and unexpanded they are stiff and erect, like porcupine quills, in contrast to the gracefully expanded and slightly drooping panicles on the healthy culms. See Fig. 1, B.

2. USTILAGO HALOPHIA Speg. An. Mus. Nac. de Buenos Aires, ser. 3, 1:58. 1902.

Sori surrounding the internodes and the rachis of the aborted inflorescence, covered at first by a grayish membrane (the host epidermis), dark-brown to black, granular to pulverulent; spores globose, ovoid to slightly irregular, yellow or yellowsh-brown to olivaceous-brown, smooth, chiefly 5-7μ in diameter, or 4-6 x 7-8μ. Fig. 2.

On Gramineae:

Distichlis spp. Idaho, Washington

Spore germination in *Ustilago halophila* has been observed on dextrose-malt-extract agar. After 18-24 hours at room temperature (21-22° C.) a germ tube begins to emerge from the spore. This elongates rather rapidly and soon becomes septate. (Usually sporidia are borne from the promycelial cells or from branches of the promycelium.) Sometimes fusions occur between cells of the promycelium. These fusions quickly give rise to infection hyphae. Fig. 2, C.

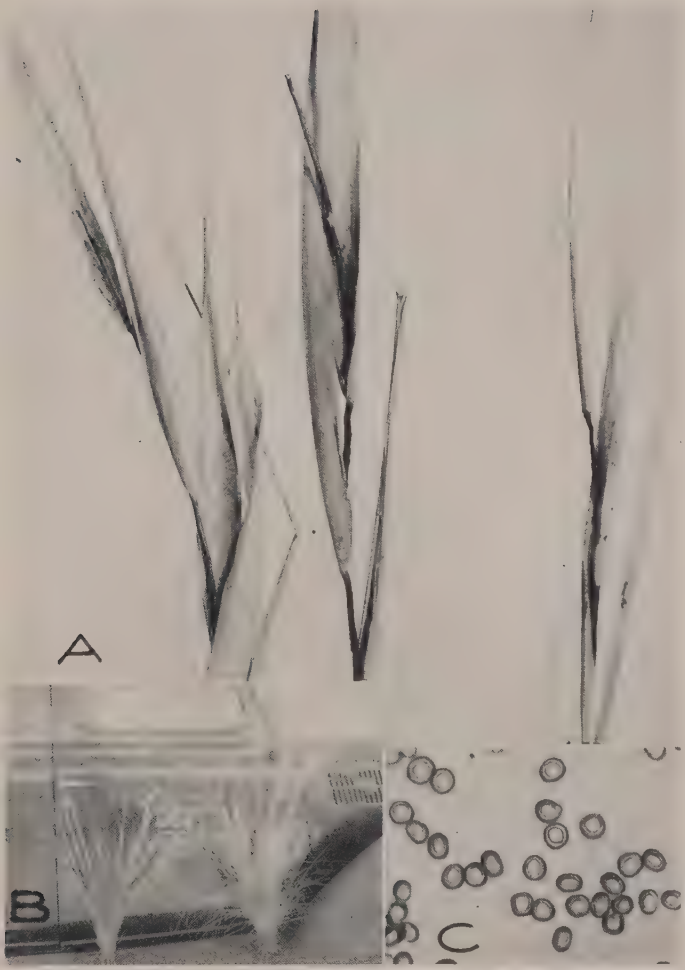

Fig. 1. Stem smut, *Ustilago numularia*: A. Habit, Indian ricegrass (*Oryzopsis hymenoides*). B. on needle grass (*Stipa comata*), healthy plant at right. Note quill-like appearance of smutted culms when immature as in plant on left. C. Spores, x approx. 900.

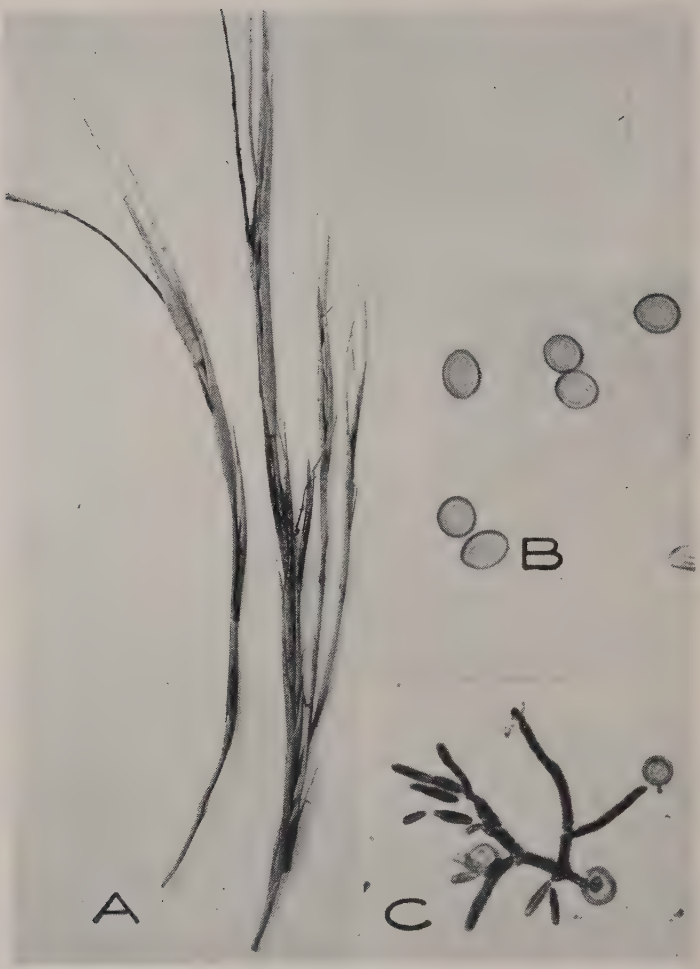

Fig. 2. Stem smut of saltgrass *Ustilago halophila*: A. Typical appearance of saltgrass (*Distichlis stricta*) affected with stem smut. B. Spores, x approx. 1000. C. Germinating spore, x approx. 900.

3. USTILAGO SPEGAZZINII Hirschh. Notas del Museo de La Plata, Botanica 4: 415-419. 1939.

Sori chiefly surrounding the internodes, but sometimes also involving more or less the inflorescence, although usually the inflorescence is entirely aborted, dark olive-brown to almost black, entirely naked except for the enveloping leaf sheaths; spores globose or subglobose, to slightly oval or even somewhat angular, provided with bipolar sub-hyaline crests consisting of a prolongation of the epispore into a group of echinulations, finely punctate to minutely echinulate (oil immersion), clear yellowish-brown to olivaceous-brown, mostly 4-6μ in diameter, or ovoid, 3.5-5 x 5-7μ. Fig. 3.

On GRAMINEAE:

Agropyron cristatum (L.) Gaertn. Washington, Oregon
Agropyron dasystachyum (Hook.) Scribn. Washington, Oregon
Agropyron inerme (Scribn. & Sm.) Rydb. Washington
Agropyron repens (L.) Beauv. Washington, Oregon, Idaho
Agropyron semicostatum (Steud.) Nees. Washington
Agropyron sibiricum (Willd.) Beauv. Washington
Agropyron spicatum (Pursh) Scribn. and Sm. Washington
Agropyron trichophorum (Link) Richt. Washington
Elymus angustus Trin. Washington
Elymus excelsus Turcz. Washington
Elymus glaucus Buckl. Washington
Melica harfordii Boland Washington
Poa nevadensis Vasey Washington
Poa palustris L. Washington
Puccinellia distans (L.) Parl. Washington
Sitanion jubatum J. G. Sm. Washington

USTILAGO SPEGAZZINII var. AGRESTIS (Sydow) G. W. Fisch. & Hirschh. Mycologia 37: (2). 236-266. 1945.

Spores dark-brown, smooth or very finely papillose, bipolar areas varying from entire apical thickenings to conspicuous, more or less lacerated crests, sub-hyaline to concolourous with the spore.

On GRAMINEAE:

Agropyron cristatum (L.) Gaetn. Washington, Oregon
Agropyron elongatum (Host) Beauv. Washington
Agropyron inerme (Scribn. & Sm.) Rydb. Washington
Agropyron intermedium (Host) Beauv. Washington
Agropyron pendulinum (Nevski) Swallen Washington
Agropyron smithii Ryd. Washington
Agropyron spicatum (Pursh) Scribn. and Sm. Washington
Agropyron trachycaulum (Link) Malte Washington, Oregon, Idaho
Agropyron trichophorum (L.) Richt. Washington

Fig. 3. Stem smut, *Ustilago spegazzinii*: A Habit, on quack grass (*Agropyron repens*). Normal culm and spike at left. B. Spores (*U. spegazzinii* var. *agrestis*), x approx. 1000.

Agropyron repens (L.) Beauv. Washington, Oregon, Idaho
Elymus canadensis L. Washington
Elymus condensatus Presl Washington
Elymus dahuricus Turcz. Washington
Poa ampla Merr. Washington
Poa juncifolia Scribn. Washington
Poa nevadensis Vasey Washington
Phalaris arundinacea L. Washington
Phleum pratense L. Washington

On plain or nutrient agar, and at room temperature (20-22° C.), spore germination of *Ustilago spegazzinii* and the variety *agrestis* commences in about 40 hours or more. A single germ tube emerges, elongates, and usually soon becomes differentiated more or less into a 3-4 celled promycelium. However, these cells have not been observed to produce primary sporidia, but instead long slender branches. Occasionally a sporidium will be formed at the tip of one or more of these branches but more often the branches elongate and re-branch, to initiate a mycelium. Very soon aerial branches begin to bear short chains of aerial sporidia. Fusions have been noted between the detached aerial sporidia.

4. USTILAGO WILLIAMSII (Griff.) Lavrov Trav. Inst. Sci. Biol. Univ. Tomsk 2:22. 1936.

Sori surrounding the upper internodes, sometimes involving also remnants of the aborted inflorescence, dark-brown to black, naked except for enclosing leaf sheaths; spores globose to sub-globose, clear yellowish-brown to dark olivaceous-brown, provided with an expospore that is smooth, but deeply cracked, forming two bipolar cap-like appendages (sometimes four), 7-10μ in diameter. Fig. 4.

On GRAMINEAE:
Oryzopsis bloomeri (Boland.) Ricker Washington
Stipa comata Trin. and Rupr. Oregon
Stipa occidentalis Thrub. Oregon
Stipa thurberiana Piper Washington, Oregon
Stipa williamsii Scribn. Washington

There are some variations in the character of the epispore of *Ustilago williamsii* on different hosts that deserve mention. In some collections on *Stipa* the spores are clear and yellowish, while in others the spores are dark brown and opaque. Sometimes the epispore is deeply cracked to form the outlines of the appendages but these are largely lacking. Other times portions of the cracked epispore have separated sufficiently to form conspicuous appendages.

Germination takes place rapidly. On dextrose malt-extract agar, at room temperature, a 3- to 4-celled promycelium emerges within 6 hours and soon develops primary sporidia or branches. Fig. 4, C.

Fig. 4. Stem smut, *Ustilago williamsii*: A. Typical appearance, on *Stipa speciosa*. B. Spores. C. Germinating spore. B and C x approx. 800.

PART TWO

LEAF SMUTS

5. USTILAGO LONGISSIMA (Schlecht.) Meyen in Pflanzenpath. p. 124. 1841.

Sori in the leaves and sheaths, linear, sometimes as much as several centimeters long, at first covered by the host epidermis which soon ruptures to expose the light brown spore-mass; spores mostly globose or subglobose, but often ovoid to elongate, clear golden-yellowish to light olivaceous, minutely and rather sparsely echinulate (oil immersion) 4-7 x 7-9 μ. Fig. 5.

On GRAMINEAE:

Glyceria elata (Nash) Hitchc. Oregon
Glyceria grandis S. Wats. Washington, Oregon, Idaho

6. USTILAGO STRIIFORMIS (Westend.) Niessl Hedwigia 15: 1. 1876.

Sori principally in the leaves and leaf sheaths, but also often extending into the inflorescence, involving the rachis, linear, dark brown to almost black, powdery, giving leaves a shredded appearance after dispersal of the spores; spores chiefly globose to subglobose or ellipsoid, rather dark olive brown, more or less prominently echinulate, chiefly 9-12μ in diameter. Fig. 6.

ON GRAMINEAE:

Agropyron inerme (Scribn. and Sm.) Rydb. Washington, Oregon
Agropyron spicatum (Pursh) Scribn. and Sm. Washington, Oregon
Agropyron striatum (Steud.) Hook. Washington
Agropyron subsecundum (Link) Hitchc. Washington
Agropyron trachycaulum (Link) Malte Washington, Oregon
Agrostis alba L. Washington, Oregon, Idaho
Agrostis castellana Boiss. and Reut. Washington
Agrostis exarata Trin. Oregon
Agrostis palustris Huds. Washington, Oregon
Agrostis stolonifera L. Washington
Agrostis tenuis Sibth. Washington, Oregon
Beckmannia syzigachne (Steud.) Fern. Oregon
Elymus canadensis L. Washington
Elymus glaucus Buckl. Washington, Oregon
Elymus sibiricus L. Washington
Holcus lanatus L. Washington, Oregon
Lolium perenne L. Oregon
Phleum pratense L. Washington, Oregon, Idaho
Poa canbyi (Scribn.) Piper Washington
Poa pratensis L. Washington, Oregon, Idaho
Sitanion jubatum J. G. Sm. Washington

Fig. 5. Brown stripe smut, *Ustilago longissima*: A. Habit, on mannagrass (*Glyceria sp.*). B. Spores, x approx. 1000.

This species is not distinguishable macroscopically from *Ustilago aculeata, U. echinata,* and *Urocystis agropyri.* Microscopically, however, *U. striiformis,* by the smaller echinulate spores, is distinct from typical *U. aculeata* and *U. echinata* (which have larger, verrucose spores), although confusing intergrades are frequently encountered. *Urocystis agropyri* is distinct by the characteristic spore balls.

Spore germination in *Ustilago striiformis* is erratic and temperamental in that collections on some grasses germinate readily while others require more or less after-ripening periods. The spores of some collections germinate with the production of branched promycelia which

Fig. 6. Stripe smut, *Ustilago striiformis*: A. Habit, on bearded wheatgrass, *Agropyron subsecundum;* B. Spores, x approx. 900.

bear ellipsoid sporidia. In other collections germinating spores have the same general aspect, but no sporidia. No doubt there is considerable heterogeneity in the species, especially with regard to germination.

7. USTILAGO ACULEATA (Ule) Liro Die Ustilagineen Finnlands. I. p. 66. 1924.

Sori having same general aspect as in *Ustilago striiformis,* from which it is indistinguishable microscopically. Spores chiefly globose to sub-globose, or occasionally somewhat elongate, usually rather dark brown, more or less verrucose, sometimes strikingly so, chiefly 14-19μ in diameter. Fig. 7.

On Gramineae:

Agropyron cristatum (L.) Gaertn. Washington
Agropyron inerme (Scribn. and Sm.) Rydb. Washington
Agropyron spicatum (Pursh) Scribn. and Sm. Washington, Oregon
Elymus canadensis L. Washington

Spore germination has been observed on dextrose-malt extract agar. After 2-3 days at room temperature a short, thick germ tube emerges which slowly develops branches. These slowly undergo further development to form a thick mat of mycelium. Sporidia have not been observed.

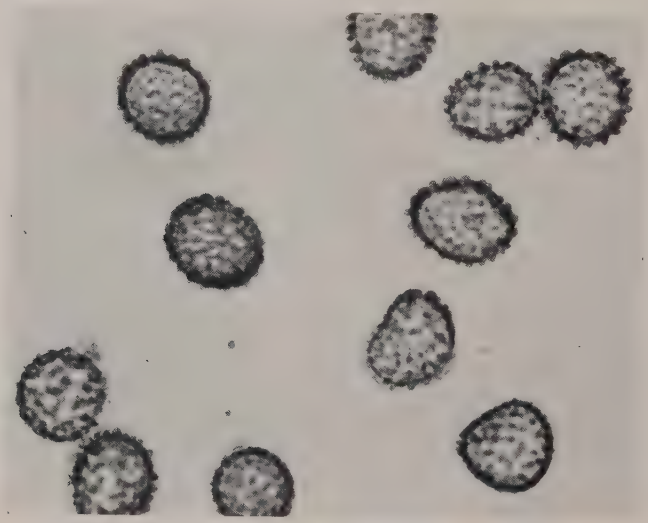

Fig. 7. Stripe smut, *Ustilago aculeata*: Spores, x approx. 1000.

8. USTILAGO ECHINATA Schroet. Abh. Schles. Abth. Nat. Med. 1869-72: 4. 1870.

Sori linear, forming long black striae in the leaves and sheaths, often confluent, especially in the aborted inflorescence, at first covered by the host epidermis but soon exposed; spores globose to sub-globose and ovoid, dark olive-brown, coarsely echinulate to verrucose, 14-16 x 16-19μ. Fig. 8.

On Gramineae:

Phalaris arundinacea L. Washington

Macroscopically, this species is very similar to the other black stripe smuts. Microscopically it is very close to and might be considered identical with *Ustilago aculeata.*

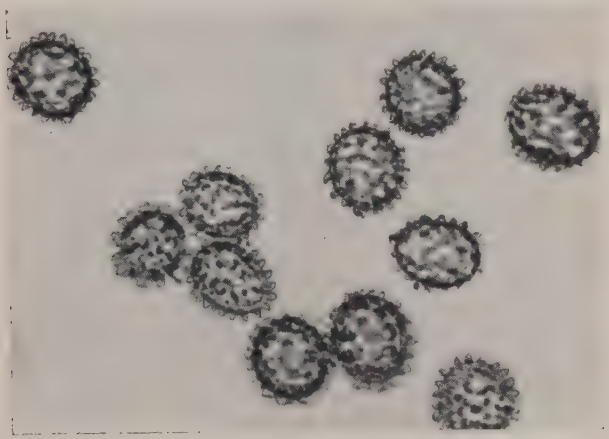

Fig. 8. Stripe smut of reed canary grass, *Ustilago echinata*: Spores, x approx. 1000.

9. USTILAGO BISTORTARUM (DC.) Koern. Hedwigia 16: 38. 1877.

Sori in the leaves, bullate, amphigenous, usually marginal and confluent but (at least in some specimens on *Polygonum viviparum*) sometimes as circular pustules scattered over entire leaf surface, at first covered by host epidermis, this soon rupturing to expose the purplish-brown spore mass; spores mostly globose to subglobose, but occasionally polygonal or oblong, light violaceous to purplish brown, minutely and densely echinulate, mostly 11-15μ in diameter. Fig. 9.

On Polygonaceae:

Polygonum bistortoides Pursh Washington

Fig. 9. Marginal leaf smut, *Ustilago bistortarum*: A. Habit, on smartweed (*Polygonum bistortoides*). B. Spores, x approx. 100.

10. UROCYSTIS AGROPYRI (Preuss) Schroet. Abh. Schles. Ges. Abth. Nat. Med. 1869-72: 7. 1869.

Urocystis tritici Koern. Hedwigia 16: 33. 1877.

Sori principally in the leaves and sheaths, but often also in the rachis of the aborted inflorescence, linear, black, at first covered by the host epidermis, frequently stunting the growth of the affected plants; spore-balls globose to elongate, composed of 1-4 dark, fertile spores and an investing layer of hyaline to brownish, smaller sterile cells, mostly 18-35 x 35-40μ; spores globose to subglobose, dark reddish-brown to olivaceous-brown, smooth, 14-20μ in diameter. Fig. 10.

On Gramineae:

Agropyron spicatum (Pursh) Scribn. & Sm. Washington, Oregon
Agropyron trachycaulum (Link) Malte Washington
Bromus carinatus Hook. and Arn. Washington
Calamagrostis canadensis (Michx.) Beauv. Oregon
Elymus condensatus Presl Washington
Elymus glaucus Buckl. Idaho, Oregon, Washington
Elymus mollis Trin. Washington
Hordeum jubatum L. Oregon
Hordeum nodosum L. Oregon
Koeleria cristata (L.) Pers. Oregon
Poa pratensis L. Washington
Poa secunda Presl Washington, Idaho
Sitanion jubatum J. G. Sm. Washington
Triticum aestivum L. Washington

The flag smut on wheat has been considered a spearate species until recently (Fischer, 1943) when the morphologic identity with flag smut on grasses was emhasized, as well as the susceptibility of grassès to wheat flag smut. For this reason the wheat flag smut (*Urocystis tritici*) is included in *U. agropyri,* the latter name having priority.

Germination of the smut on grasses has not been observed. On wheat, spore germination seems to be best induced by sowing the spore balls on water. Generally, in 3-5 days each spore produces a short thick promycelium at the end of which is borne a cluster of 3-5 or more hyaline cylindrical sporidia.

11. ENTYLOMA IRREGULARE Johans. Ofversigt af Vetenskaps-Akad. Förhandl. 1884: 159. 1885.

Sori chiefly in the leaves but also occasionally in the rachis of the inflorescence, greenish-black, in the form of irregularly circular or oval spots, .5-2 mm. in diameter, long covered by the epidermis; spores subglobose, oblong, to polyhedral, tending to adhere in irregular groups, light to dark olivaceous-brown, rather thick-walled, smooth, 7-11 x 8-17μ. Fig. 11.

Fig. 10. Flag smut, *Urocystis agropyri:* A. Habit, on Baart wheat. B. Typical spore-balls, x approx. 800.

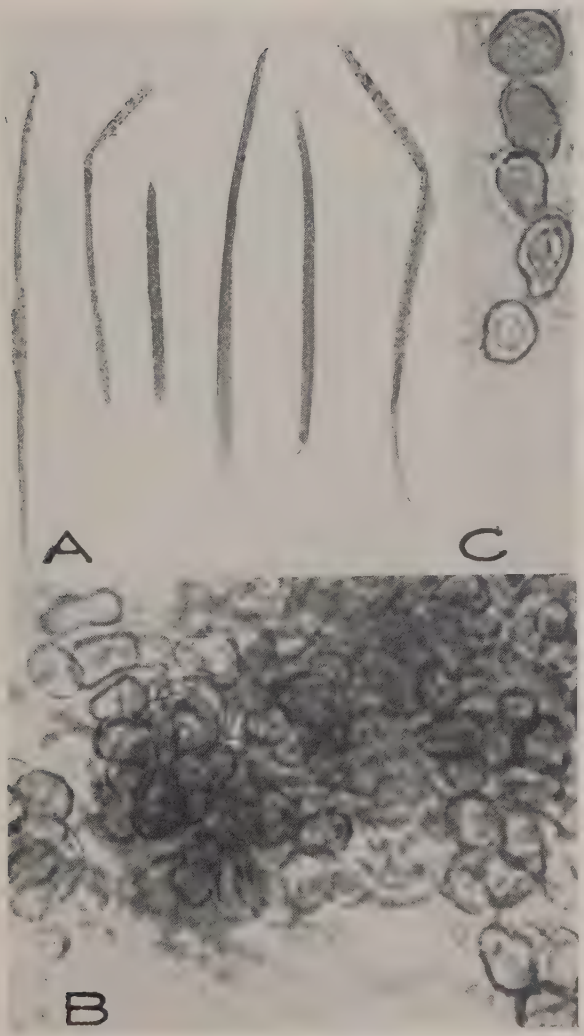

Fig. 11. Spot smut of bluegrasses, *Entyloma irregulare*: A. Habit on Kentucky bluegrass, *Poa pratensis*. B. Spore-mass, taken from leaf tissues of *Poa compressa*. C. Individual spores, from *Poa juncifolia*. B. and C x approx. 1000.

On Gramineae:

Poa annua L. Oregon
Poa compressa L. Oregon
Poa juncifolia Scribn. Oregon
Poa pratensis L. Washington, Oregon
Poa vaseyochloa Scribn. Washington

There is some variation in different collections of *Entyloma* on grasses, with regard to spore size and shape, wall thickness, color intensity, and the tendency to adhere in groups. For this reason it is frequently difficult to determine with reasonable certainty the species, because they are delimited on the basis of just such variable characters. Sometimes a collection will have the size and shape for one species, but will have the color and wall thickness supposedly restricted to another species. Other times collections will be encountered in which the spores are free or only slightly tending to be agglutinated, but will lack color or wall character necessary to make positive specific determination. For this reason it seems probable that such species as *E. crastophilum* Sacc., *E. irregulare, E. speciosum* Schröt. and P. Henn., and possibly *E. lineatum* (Cooke) Davis are not really distinct species, but rather represent ecological variations within a composite species.

12. ENTYLOMA RANUNCULI (Bon.) Schroet. in Cohn, Beitr. Z. Biol. d. Pfl. 2: 370. 1877.

Sori in the leaves, amphigenous, forming spots, usually angular because delimited by the larger veins, pale yellowish brown to pinkish, more or less caeomoid on under surface because of numerous individual small masses of conidia; spores globose, pale lemon yellow, with thin hyaline envelope, smooth, mostly 10-14μ in diameter; condia fusiform, often bent or curved at one end, hyaline, 15-30 x 2.5-3μ. Fig. 12.

On Ranunculaceae:

Ranunculus bongardi Greene Oregon
Ranunculus macounii var. *oreganus* (Gray) Davis Washington
Ranunculus sceleratus var. *multifidus* Nutt. Washington

13. ENTYLOMA ARNICALE Ell. and Ev. Bull. Torr. Bot. 22: 57. 1895.

Sori in the leaves, forming circular to angular yellowish-brown to reddish-brown spots, amphigenous, 2-8 mm. in diameter or occasionally larger; spores globose to subglobose or ovoid, pale yellow to pale yellowish-brown, often with irregular hyaline envelope, projections of which sometimes give the appearance of hyaline papillae or tubercles, thick-walled, smooth, 11-15μ in diameter. Fig. 13.

On Compositae:

Arnica cordifolia Hook. Idaho
Arnica latifolia Bong. Washington
Arnica mollis Hook. Washington
Arnica sp. Oregon

Fig. 12. Buttercup smut, *Entyloma ranunculi*: A. Habit, on buttercup (*Ranunculus* sp.). B. Spores. C. Conidia. B. and C. x approx. 1000.

This smut has been reported in some of the taxonomic works to form a conidial stage on the upper surface of the spots, sometimes in rather great abundance. Measurements for the conidia have been given by Clinton (1906) as 18-28 x 3μ hyaline. We have not observed them in the specimens studied.

14. ENTYLOMA COMPOSITARUM Farl. Bot. Gaz. 8: 275. 1883.

Sori in the leaves, producing spots, amphigenous, variable in size according to host and collection, sometimes very small inconspicuous yellowish spots, in other cases forming large confluent yellowish-brown areas, often with conidial growth evident on both surfaces as numerous

Fig. 13. Spot or leaf smut of Arnica, *Entyloma arnicale*: Habit, on *Arnica* sp., showing typical leaf-spot appearance.

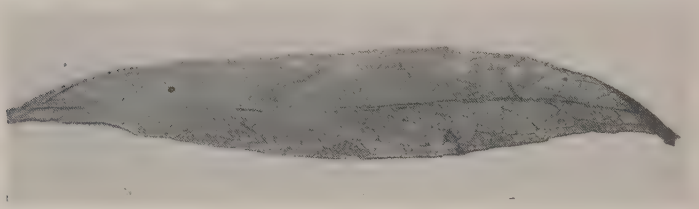

Fig. 14. Spot smut of composites, *Entyloma compositarum*: Habit, on *Aster paniculatus*.

small whitish pustule-like areas over the spots and superficially resembling the cluster-cups of rusts; spores globose, subglobose, to ovate, hyaline to pale greenish-yellow, thin-walled, smooth, mostly 9-12μ in diameter; conidia fusiform to falcate, hyaline, 14-18 x 2.5μ. Fig. 14.

On Compositae:

Erigeron elatus (Hook.) Greene Washington
Erigeron salsuginosus (Richards) Gray Washington
Madia sp. Oregon

15. TUBERCINIA TRIENTALIS Berk. and Br. Ann. Mag. Nat. Hist. II. 5: 464. 1850.

Tubercinia clintoniae Kom. Jacz.-Kom.-Tranz. Fungi Rossiae No. 260. 1899.

Sori in the leaves, petioles, and stems, variable in size and often confluent, lead-colored to blackish, long covered by the epidermis, amphigenous, but with lower surface of infected leaves sometimes more or less covered by a whitish bloom consisting largely of conidiophores and conidia; spore-balls mostly globose or subglobose, occasionally ovate to oblong, subopaque, rather dark chestnut-brown to smoky-brown, more or less invested in a layer of hyaline hyphal fragments, 24-56 x 28-70μ; spores firmly united, subglobose to ovate or oblong, often polyhedral from compression, light chestnut-brown to smoky-brown, subopaque, smooth, mostly 9-12 x 14-17μ; conidia oblong to ovate, hyaline, mostly 5-7 x 8-14μ. Fig. 15.

On Liliaceae:

Smilacina stellata (L.) Desf. Idaho
Streptopus roseus Michx. British Columbia

On Primulaceae:

Trientalis latifolia Hook. Washington, Oregon

The consolidation of *Tuburcinia clintoniae* with *T. trientalis,* as indicated above, is based on studies of a single collection of the former species (Ellis and Everhart's Fungi Columbiani, No. 1789, on *Streptopus roseus,* Glacier, B.C.). This collection differed from collections of *T. trientalis* only in having slightly lighter colored spore-balls and spores, —hardly sufficient difference to merit distinction as a separate species.

16. WHETZELLA WALDSTEINIAE (Pk.) Zundel Mycologia 37 (3): (in press) 1945.

Urocystis waldsteiniae Pk. Ann. Rept. N. Y. State Museum 46: 112. 1893.

Sori on upper surface of leaves, bullate, linear, superimposed above the veins, covered by a brittle but comparatively thick membrane of fungous tissue which splits lengthwise to expose the nearly black sporemass; spores variously shaped: globose, subglobose, ovoid, angular, even sometimes lunate, fragile, easily collapsing, often in pairs or threes and occasionally more, simulating spore-balls, light olivaceous-brown to chestnut-brown, smooth, 10-14 x 10-16μ. Fig. 16.

On Rosaceae:

Geum triflorum var. *ciliatum* (Pursh) Fassett Washington

Fig. 15. *Tuburcinia trientalis*: A. Habit, on *Trientalis americana*. The blackish areas are the sori; the whitish areas represent conidial production. B. Typical spore-balls, x approx. 300.

This smut, having been proved not to be a *Urocystis* as originally described by Peck is the type species of a new genus, *Whetzelia*. This information has just been communicated to us by Dr. G. L. Zundel, as well as the binomial and literature citation given above.

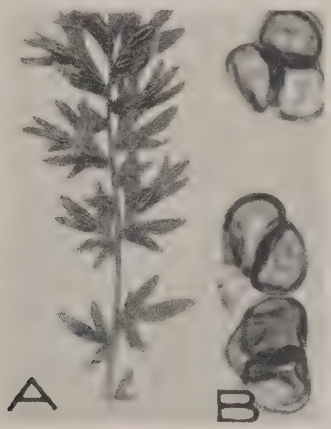

Fig. 16. *Whetzelia waldsteiniae*: A Habit, on *Geum triflorum* var. *ciliatum*. B. Spore-balls, approx. 800.

17. DOASSANSIA ALISMATIS (Nees) Coru. Ann. Sci. Nat. VI. 15: 285. 1883.

Sori in the leaves, forming amphigenous yellowish-brown to greenish-brown spots, 3-10 mm. in diameter, often confluent; spore balls visible with hand lens as numerous, roundish, pycnidia-like elevations, mostly in the pallisade parenchyma, globose, subglobose, to oblong, with a distinct cortex of chestnut-brown, elongate cells, radially disposed, and enclosing the spore-mass, 140-180μ in diameter, cortical cells 5-8 x 10-18μ; spores globose to polyhedral from compression, thin walled, pale chestnut brown, smooth, 8-10μ in diameter. Fig. 17.

On Alismaceae:

Alisma plantago-aquatica L. Washington

18. DOASSANSIA MARTIANOFFIANA (Thuem.) Schroet. Krypt. Flora Schles. 31: 287. 1887.

Sori in the leaves, forming minute chlorotic spots, often confluent, to form larger areas, amphigenous, with spore-balls easily visible (with hand lens) as numerous, globose, pycnidium-like bodies especially over the under surface of the leaf; spore balls mostly globose to subglobose

Fig. 17. *Doassansia alismatis*: A. Habit, on water-plantain *Alisma plantago-aquatica*. B. Cross-section of spore-balls. Note outer sterile cortex, and center mass of thin-walled spores, x approx. 200.

or elongate, 105-150μ in diameter with a distinct cortex of sterile, light chestnut-brown, radially-arranged cells measuring 7-10 x 9-13μ; spores mostly globose to ovate or polyhedral, pale yellowish-brown, smooth, 10-14μ in diameter.

On Potamogetonaceae:

Potamogeton sp. Washington

PART THREE

INFLORESCENCE SMUTS

19. USTILAGO NUDA (Jens.) Rostr. Tidsskrift f. Landokonomi 8: 745. 1889.

Ustilago tritici (Pers.) Rostr. Overs. Kong Danske Vidensk. Selsk. Forh. 1890: 15. March, 1890.

Ustilago tritici Jens. in Kell. and Swing. Ann. Rept. Kan. Agric. Expt. Sta. 2:262. June, 1890.

Fig. 18. Loose smut of wheat and barley, *Ustilago nuda*: A. Habit, on wheat. B. Spores, x approx. 1000.

Ustilago nuda Kell. and Swing. Ann. Rept. Kan. Agric. Expt. Sta. 2: 277. June, 1890.

Sori in the spikelets, very loose and dusty, olivaceous-brown to almost black, usually entirely destroying the floral parts, leaving behind the naked rachis; spores globose to subglobose or elongate, clear olivaceous-brown, lighter on one side, minutely echinulate (more prominent on clear side), chiefly 5-7μ in diameter. Fig. 18.

On Gramineae:

Agropyron sibircum (Willd.) Beauv. Washington
Hordeum vulgare L. Washington, Oregon, Idaho
Triticum aestivum L. Washington, Oregon, Idaho
Triticum spelta L. Oregon

On a variety of media the aspect of spore germination is the same. A slender germ tube emerges from the spore and begins to branch. The branches elongate and re-branch and the process continues, forming a mycelium.

The loose smut of wheat and the loose smut of barley have generally been considered as separate species. However, as has been recently emphasized (Fischer, 1943) these two smuts are identical in their morphology, life history, and control, and therefore should be considered as one morphologic species. The binomial *Ustilago nuda* seems to have priority in accordance with International Rules of Botanical nomenclature.

20. USTILAGO SITANII G. W. Fisch. Mycolgia 30: 385-395. 1938.

Sori principally in the distorted inflorescence, more or less destroying it, involving chiefly the awns, glumes, and other floral parts, but also forming long and short striae in the upper leaves and leaf sheaths, early naked and dusty, revealing the brown spore-mass; spores globose to ovate, light olive-brown, uniformly rather thick-walled, minutely echinulate, 3.5-5 x 3.5-7μ, mostly 4x5μ. Fig. 19.

On Gramineae:

Sitanion jubatum J.G.Sm. Washington, Oregon
Sitanion hanseni (Scribn.) J.G.Sm. Washington Oregon
Hordeum nodosum L. Washington
Hordeum jabatum var. *caespitosum* (Scribn.) Hitchc. Washington

Spore germination, on a variety of media, is direct. That is, the germ tube develops directly into a mycelium, without production of sporidia.

21. USTILAGO RESIDUA Clint. Jour. Myc. 8: 133. 1902.

Sori destroying the entire inflorescence, at first enclosed by the leaf sheaths, profuse, dusty, olive-brown, with shredded remains of

Fig. 19. Loose smut of squirreltail grass, *Ustilago sitanii*: A. Habit, on big squirreltail (*Sitanion jubatum*). B. Spores, x 1000.

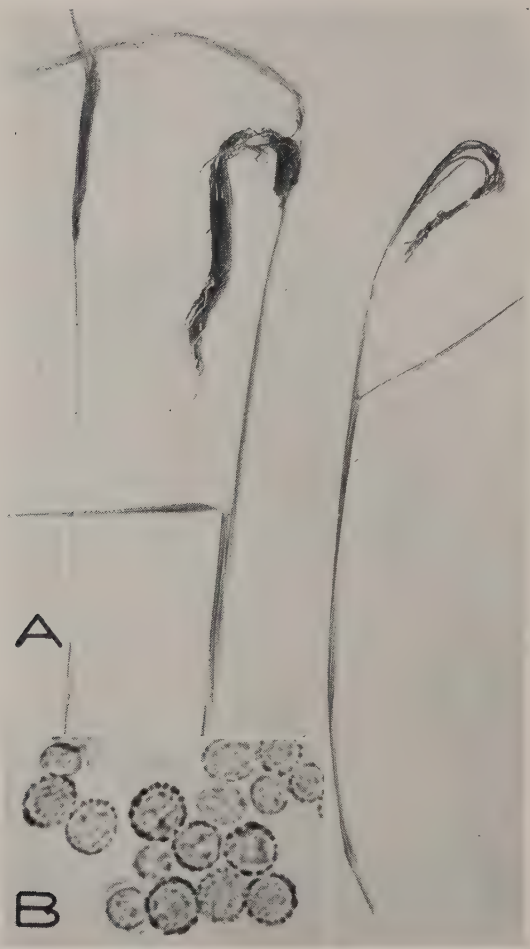

Fig. 20. Loose smut of oatgrass, *Ustilago residua*: A. Habit, on California oatgrass (*Danthonia californica*). B. Spores, x approx. 1000.

host tissue; spores globose to irregularly elongate, golden-yellow to light olive-brown, prominently granular-verrucose, 5-7 x 7-10μ. Fig. 20.

On Gramineae:

Danthonia californica Boland. Washington, Oregon

22. USTILAGO NEGLECTA Niessl in Rabenhorst, Fungi Europaei, 1200. 1868.

Sori in the ovaries, usually involving all of the flowers of the spike, at first more or less hidden by the glumes, dusty, dark purple-brown; spores light reddish brown to brown, irregularly globose or ovoid and elongate, strikingly echinulate, 7-11 x 9-12μ. Fig. 21.

On Gramineae:

Setaria lutescens (Weigel) F. T. Hubb. Washington

Fig. 21. Fox-tail smut, *Ustilago neglecta*: A. Habit, on fox-tail grass, (*Setaria lutescens*) B. Spores, x approx. 800.

23. USTILAGO MULFORDIANA Ell. and Ev. Bull. Torrey Bot. Club 22: 362. 1895.

Sori in the aborted inflorescence, more or less concealed by the enveloping leaves, dark-brown to almost black, at first covered by a very thin whitish membrane (the host epidermis); spores dark olivaceous-brown, opaque, irregularly globose to ovoid, 12-19μ in diameter, epispore thick and coarsely echinulate. Fig. 22.

On Gramineae:

Festuca dertonensis (All.) Aschers. and Graebn. Washington
Festuca microstachys Nutt. Washington
Festuca octoflora Walt. Washington, Oregon, Idaho

Festuca pacifica Piper Washington, Oregon
Festuca reflexa Buckl. Washington

Fig. 22. Fescue smut, *Ustilago mulfordiana*: A. Habit, *Festuca pacifica*. B. Spores, x approx. 800.

24. USTILAGO AVENAE (Pers.) Rostr. Overs. K. Danske Vid. Selsk. Forh. 1890: 13. 1890.

Ustilago perennans Rostr. Overs. K. Danske Vid. Selsk. Forh. 1890: 15. 1890.

Ustilago nigra Tapke Phytopath. 22: 869. 1932.

Sori in the inflorescence, especially in the ovaries, more or less

Fig. 23. Loose smut, *Ustilago avenae*: A. Habit, on tall oatgrass (*Arrhenatherum elatius*) (left), and cultivated oats. B. Spores, x approx. 1000.

destroying all the floral parts, forming a dark-brown to almost black, usually loose, spore-mass; spores globose to sub-globose or elongate, yellowish-brown to olive-brown, lighter colored on one side, minutely echinuate, echinulations usually more prominent on the lighter colored side, chiefly 5-7 x 6-9μ. Fig. 23.

On Gramineae:

Arrhenatherum elatius (L.) Presl Washington, Oregon, Idaho
Avena fatua L. Washington
Avena sativa L. Washington, Oregon, Idaho
Hordeum vulgare L. Washington

Spore germination is characterized by the production of a 3- or 4-celled promycelium, bearing sporidia from each cell.

This morphological species includes three distinct physiologic entities: the loose smut of oats (*Ustilago avenae*), the loose smut of tall oatgrass (*U. perennans*), and the black loose smut of barley (*U. nigra*). It is unfortunate that International Rules of Botanical nomenclature necessitate the application of *U. avenae* to this combined species since this name might be taken to indicate specialization to oats, or *Avena* spp. The reasons for the consolidation of these three smuts into a single morphological species have been given elsewhere (Fischer, 1943).

25. USTILAGO BULLATA Berk. in Hooker, W. J. Flora of New Zealand 2: 196. 1855.

Ustilago bromivora (Tul) Fisch, v. Waldh. Bull. Soc. Nat. Mosc. 40: 252. 1867.

Ustilago lorentziana Thuem. Flora 63: 30. 1880.

Sori in the spikelets, bullate, sometimes entirely involving the glumes but more often only partially so, at first enclosed by a greyish to greenish membrane (the host epidermis) of varying strength according to host, but which sooner or later ruptures, exposing the powdery dark-brown to purple-black spore-mass; spores mostly globose to subglobose, but sometimes, especially in agglutinated specimens, tending to be irregular or polyhedral, usually dark brown or olive-brown, with an epispore varying from minutely echinulate to granular-verrucose, 5-14μ in diameter, more often 7-9μ, not including the occasional elongate and irregular spores nearly always present. Fig. 24.

On Gramineae:

Agropyron caninum (L.) Beauv. Washington
Agropyron cristatum (L.) Gaertn. Washington, Oregon
Agropyron dasystachyum (Hook.) Scribn. Washington
Agropyron inerme (Scribn. and Sm.) Rydb. Washington
Agropyron orientale var. *lasianthum* (Boiss.) Washington
Agropyron spicatum (Pursh) Scribn. and Sm. Washington
Agropyron subsecundum (Link) Hitchc. Washington
Agropyron trachycaulum (Link) Malte Washington, Oregon, Idaho
Bromus anomalus Rupr. Washington, Idaho
Bromus brizaeformis Fisch. and Mey. Washington, Idaho
Bromus carinatus Hook. and Arn. Washington, Oregon

Fig. 24. Head smut, *Ustilago bullata*: A. Habit, on rescue grass (*Bromus catharticus*) (left), crested wheatgrass (*Agropyron cristatum*) (center), and slender wheatgrass (*Agroypron trachycaulum*). B. Spores, x approx. 1000.

Bromus catharticus Vahl. Washington, Oregon, Idaho
Bromus ciliatus L. Washington
Bromus commutatus Schrad. Washington, Oregon, Idaho
Bromus erectus Huds. Washington, Oregon, Idaho
Bromus inermis Leyss. Washington
Bromus japonicus Thunb. Washington
Bromus marginatus Steud. Washington, Oregon, Idaho
Bromus mollis L. Washington, Oregon, Idaho
Bromus purgans L. Washington
Bromus racemosus L. Washington
Bromus rigidus Roth Washington, Oregon
Bromus secalinus L. Washington, Oregon
Bromus secalinus var. *velutinus* (Schrad.) Koch Washington, Oregon
Bromus sibiricus Drob. Washington
Bromus squarrosus L. Washington
Bromus sterilis L. Washington
Bromus tectorum L. Washington, Oregon, Idaho
Bromus tomentellus Bois. Washington
Bromus vulgaris (Hook.) Shear Washington
Elymus canadensis L. Washington, Oregon
Elymus excelsus Turcz. Washington
Elymus glaucus Buckl. Washington
Elymus junceus Fisch. Washington
Elymus sibiricus L. Washington
Festuca idahoensis Elmer Washington
Hordeum jubatum L. Washington, Oregon, Idaho
Hordeum nodosum L. Washington, Oregon, Idaho

Spore germination usually takes place readiy. Among collections from the various hosts considerable variation may be seen in the appearance of germinating spores. From one to three promycelia emerge from each spore. The promycelia are 1-3-celled, and bear ellipsoid to oval or oblong sporidia at the tips and cross-walls.

26. USTILAGO HORDEI (Pers.) Lagh. Mitt. Badeschen Bot. Ver. p. 70. 1889.

Ustilago kolleri Wille Bot. Notiser 1893: 10. 1893.

Ustilago levis Magn. Ber. Natur-Wiss. Mediz. Ver. Innsbruck 21: 22. 1894.

Sori in the spikelets, rather hard and compact, more or less concealed by the glumes on some hosts, on other hosts the glumes are largely consumed; spores globose to sub-globose, light olive-brown to brown, lighter colored on one side, smooth, 5-8μ in diameter. Fig. 25.

On Gramineae:

Agropyron caninum (L.) Beauv. Washington
Agropyron cristatum (L.) Gaertn. Washington

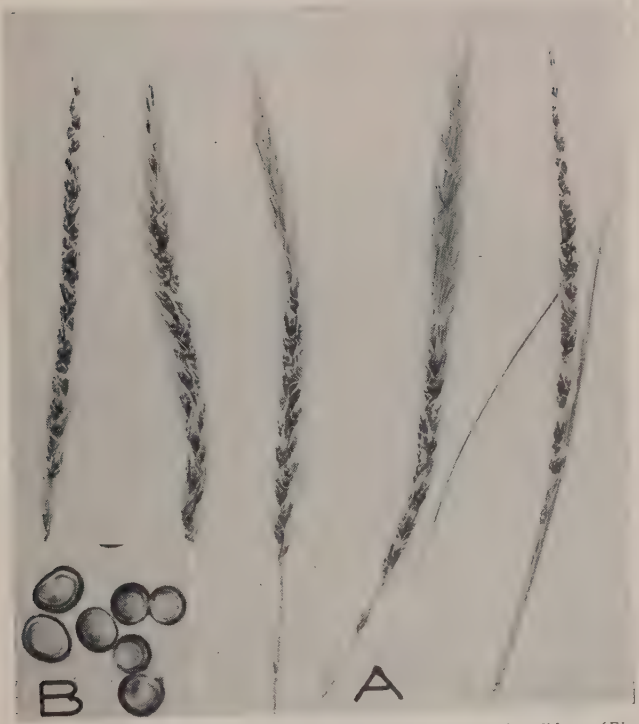

Fig. 25. Covered smut, *Ustilago hordei*: A. Habit, on Canada wild-rye (*Elymus canadensis*). B. Spores, x approx. 1000.

Avena byzantina C. Koch Washington, Oregon
Avena fatua L. Washington, Oregon
Avena sativa L. Washington, Oregon, Idaho
Elymus canadensis L. Washington
Elymus glaucus Buckl. Washington
Hordeum vulgare L. Washington, Oregon, Idaho

Spore germination is characterized by the production of 3- or 4-celled promycelia, each cell bearing sporidia. In the case of 3-celled promycelia the spore acts as the fourth cell and produces sporidia.

Ustilago hordei, as given here, includes the common covered smut of barley, and the common covered smut of oats (*Ustilago levis*). As has already been shown (Fischer, 1943), these two smuts are morphologically indistinguishable and therefore should not be considered as

spearate species. It seems logical that there is no more reason to consider the smut on oats and barley as distinct species than the same smut on *Agropyron* and on *Elymus*.

27. CINTRACTIA CARICIS (Pers.) Magn. Abh. Bot. Ver. Prov. Brand. 37: 79. 1896.

Sori in the ovaries, globose, very indurate, at first concealed more

Fig. 26. Common sedge smut, *Cintractia caricis*: A. Habit, on *Carex podocarpa*. B. Spores, x approx. 1000.

or less by the perigyniun, covered by a brittle whitish membrane of fungous tissue which soon flakes away to expose the black spore-mass; spores globose, subglobose, to polygonal, opaque, dark olive-brown to dark reddish-brown, apparently smooth but under oil immersion indistinctly and densely punctate, mostly 16-21μ in diameter. Fig. 26.

On Cyperaceae:

Carex aquatilis Wahl. Idaho
Carex douglasii Boott Washington, Oregon
Carex geyeri Boott Washington
Carex podocarpa R. Br. Idaho

28. FARYSIA OLIVACEA (DC.) Syd. Ann. Myc. 17: 41. 1919.

Sori in the ovaries, at first more or less concealed by the perigynium, later expanding into a fluffy dark olive-brown mass of spores and capillitium-like threads; spores quite variable in shape, globose to ellipsoid with truncate ends, olive brown, deeply verrucose, 5-8 x 7-14μ. Fig. 27.

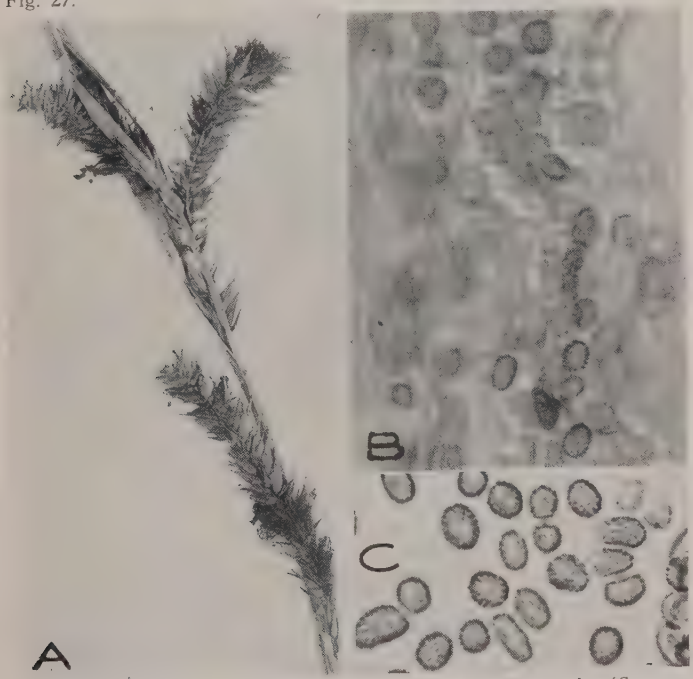

Fig. 27. Thread smut, *Farysia olivacea*: A. Habit, on swamp sedge (*Carex exsiccata*). B. Portion of a single "elater" or capillitial thread, x approx. 500. C. Spores, x approx. 800.

On Cyperaceae:

Carex rostrata Stokes Washington

This smut, along with others in the same genus, has a very interesting method of spore formation. The spores are borne in long chains, converted from long parallel hyphae, and the "elaters" or capillitium-like threads characteristic of this smut are merely long bundles of remnants of these spore-bearing hyphae which were not consumed in the process of spore formation. Fig. 27, B.

29. USTILAGO UTRICULOSA (Nees) Tul. Ann. Sci. Nat. III. 7: 102. 1847.

Sori in the ovaries, ovoid, at first covered by a thin membrane (the epidermis of the ovary) which soon ruptures to expose the pow-

Fig. 28. Smartweed smut, *Ustilago utriculosa*: A. Habit, on *Polygonum pennsylvanicum*, healthy inflorescence at right. B. Spores, x approx. 1100.

dery violaceous-brown spore-mass; spores globose or subglobose, clear violaceous, with reticulate epispore (composed of rather large, deep, polygonal reticulations), mostly 8-12μ in diameter. Fig. 28.

On Polygonaceae:

Polygonum persicaria L. Washington, Oregon

In water, at 22-25° C. spore germination usually begins in 7-8 hours. A 4-celled promycelium is produced and small hyaline eliptical sporidia are budded from the cells.

30. USTILAGO PUNCTATA Clint. N. Amer. Flora 7(1): 23. 1906.

Fig. 29. *Ustilago punctata*: A. Habit, on *Polygonum alpinum;* distorted inflorescence at left, mid-vein sori at right. B. Spores, x approx. 800.

Sori in the usually aborted inflorescence, or occasionally in the mid-vein region of the upper leaves, rather large, thick and gall-like, spore-mass purplish-black, dusty to semi-agglutinated; spores globose, subglobose, ovoid, or occasionally elongate, rather dusky purple to violaceous-brown, deeply and abundantly pitted (oil immersion) and often appearing minutely reticulate, or even slightly cerebriform, mostly 14-17μ in diameter. Fig. 29.

On POLYGONACEAE:

Polygonum alpinum All. Oregon
Polygonum newberryi Small Washington

31. SPHACELOTHECA HYDROPIPERIS (Schum.) D. By. Verg. Morph. u. Biol. d. Pilze 187. 1884.

Sphacelotheca hydropiperis var. *borealis* Clint. Proc. Bost. Soc. Nat. Hist. 31: 395. 1904.

Sphacelotheca borealis (Clint.) Schellenb. Ann. Myc. 5: 386. 1907.

Ustilago bistortarum var. *inflorescentiae* Trel. Harriman Alaska Exped. Crypt. Bot. 35. 1904.

Sphacelotheca inflorescentiae (Trel.) Jaap Ann. Mycol. 6: 194. 1908.

Sori in the ovaries, ovate-cylindrical, at first covered by a membrane of fungous tissue which soon ruptures to expose the dark purplish-brown to purplish-black spore-mass, in the center of which is a more or less distinct columella; spores mostly globose or subglobose, occasionally more elongate or irregular, pale violaceous-brown to violet, abundantly and minutely verrucose, sometimes appearing almost smooth, 9-14μ in diameter; sterile cells (remnants of the membrane) hyaline, globose to polygonal, thick-walled, mostly 12-17μ in diameter. Fig. 30.

ON POLYGONACEAE:

Polygonum bistortoides Pursh Washington
Polygonum hydropiper L. Washington, Oregon

The variety *borealis* or the species *Sphacelotheca borealis* listed above, is supposed to be distinct from *S. hydropiperis* by its more evident columella, and paler, somewhat smaller spores. A study of specimens from the United States and Europe (including the type material of the variety *borealis*) indicates strongly that the species and its variety are really only extremes of variation and that there are intergrades. For this reason *S. hydropiperis* var. *borealis* and *S. borealis* are listed as synonyms above. Similarly *S. inflorescentiae* is also listed as a synonym of *S. hydropiperis,* it being scarcely if at all distinguishable from the latter species.

32. SPHACELOTHECA DESTRUENS (Schlecht.) Stevenson and A. G. Johnson. Phytopath. 34: 613. 1944.

Sphacelotheca panici-miliacei (Pers.) Bub. Houby Ceske 2:27. 1912.

Fig. 30. Kernel smut of smartweed, *Sphacelotheca hydropiperis*: A. Habit, on smartweed (*Polygonum hydropiper*). B. Spores, x approx. 800.

Sori in the inflorescence, destroying it completely except for numerous long fibres remaining (the vascular bundles of the host), at first covered with a tough whitish membrane of fungous tissue, this rupturing irregularly to expose the dusty, dark-brown spore-mass; spores chiefly globose to subglobose, light olive-brown, apparently smooth but under oil immersion evidently more or less punctate, 7-10μ in diameter. Fig. 31.

On Gramineae:.

Panicum miliaceum L. Washington, Oregon

Spores germinating on nutrient agars at room temperature, generally produce a four-celled promycelium, from the cells of which ovoid to elliptical sporidia are budded. Fig. 31, C.

Fig. 31. Millet smut, *Sphacelotheca destruens*: A. Habit, on millet (*Panicum miliaceum*). B. Spores. C. Germinating spore. B and C x approx. 1000.

33. SPHACELOTHECA REILIANA (Kuehn) Clint. Journ. Myc. 8: 141. 1902.

Sorosporium reilianum McAlp. Smuts of Australia p. 181. 1910.

Sori large or small, prominent, in both staminate and pistillate inflorescence, dark brown, dusty, with long shredded remnants of vascular bundles remaining after spore dispersal, at first covered by membrane of fungous tissue, remnants of which are sometimes seen with the spores as subglobose to oblong groups of hyaline or pale brown sterile cells; spores globose to subglobose or ovoid, light to dark reddish-brown, opaque, abundantly but minutely echinulate, 9-12μ in diameter. Fig. 32.

On Gramineae:

Zea mays L. Washington, Oregon, Idaho

This smut has been juggled from *Ustilago* to *Cintractia,* to *Sphacelotheca,* to *Sorosporium* and back to *Sphacelotheca* again. True spore balls are rarely, if ever, found in mature specimens, and we have not even found them in very young material; hence it seems that the fungus in question is not a *Sorosporium* and is retained in the genus *Sphacelotheca.*

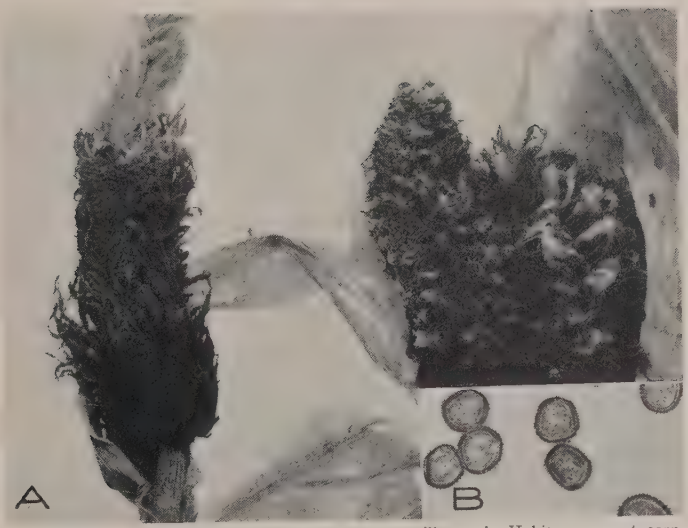

Fig. 32. Head smut of corn, *Sphacelotheca reiliana*: A. Habit, on sweet corn. Tassel infection at left; cob infection at right. B. Spores, x approx. 700.

In other parts of the United States sorghums are attacked, as well as corn.

In the process of spore germination a 3- to 4-celled promycelium is formed, from the cells of which are budded numerous, small, ovoid to ellipsoid conidia.

34. SOROSPORIUM SYNTHERISMAE (Pk.) Farl. Farl. and Seym. Host Index N. Am. Fungi 152. 1891.

Sori consuming the entire inflorescence, leaving only shredded remains of vascular bundles, at first covered by a yellowish membrane of fungous tissue which soon ruptures irregularly to expose the dark brown, dusty spore-mass; spore balls globose to oblong, dark brown, 35-70 x 70-105μ, spores globose, subglobose to elongate, olive brown, minutely verrucose, 8-11μ in diameter. Fig. 33.

On Gramineae:

Cenchrus pauciflorus Benth. Washington, Oregon

Panicum dichotomiflorum Michx. Idaho

Spores germinate readily on nutrient agar, usually commencing in 24-36 hours at room temperature. One or two 2-3 celled promycelia emerge from the spore; usually sporidia are budded off the cells of the promycelium, although frequently fusions occur between the cells and give rise directly to infection hyphae. Fig. 33, D.

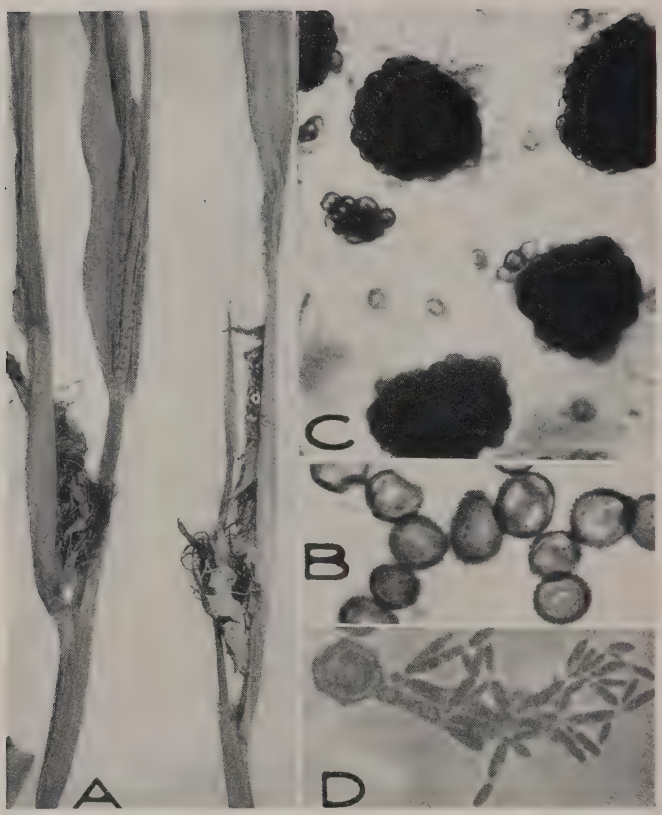

Fig. 33. Loose smut, *Sorosporium syntherismae*: A. Habit, on panic grass (*Panicum dichotomiflorum*). B. Spores, x approx. 1000. C. Spore balls, x approx. 300. D. Germinating spore, x approx. 1000.

35. SOROSPORIUM CONSANGUINEUM Ell. and Ev. Jour. Myc. 3: 56. 1887.

Sori in the ovaries, replacing the seeds, cylindric, and short enough to be almost entirely hidden by the glumes, at first covered by a thin, fragile membrane of fungous tissue; spore-balls mostly globose to subglobose, or oblong, dark brown, firm, eventually breaking up and releasing the spores individually or in very small groups, 35-70 x 50-120μ; spores chiefly pentagonal or hexagonal from compression in the spore balls, olive brown, subopaque, those from exterior of spore ball minute-

ly verrucose to echinulate, those from interior punctate to almost smooth, mostly 9-11μ in diameter. Fig. 34.

On Gramineae:

Aristida longiseta Steud. Washington, Idaho

Spore germination takes place over night on nutrient agar, and at room temperature, producing 3- to 4-celled promycelia, each cell budding off sporidia.

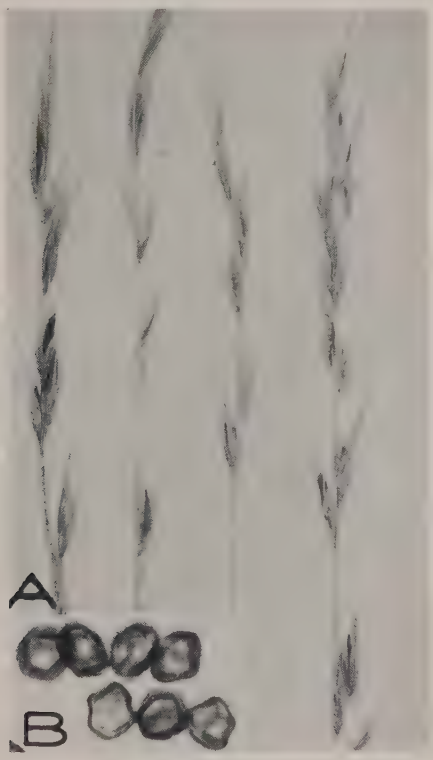

Fig. 34. Kernel smut, *Sorosporium consanguineum*: A. Habit, on three-awn grass (*Aristida longiseta*). B. Spores, x approx. 800.

36. SPHACELOTHECA SORGHI (Lk.) Clint. Jour. Myc. 8: 140. 1902.

Sori in the ovaries, replacing the seeds, oblong-cylindrical to subconical, covered by a firm membrane of fungous tissue which is almost

concolorous with the rest of the inflorescence, and which ruptures at the top, revealing the dark-brown spore-mass and the central columella of host tissue; spores chiefly globose to subglobose, olivaceous-brown, tending to be somewhat lighter on two sides, apparently smooth, but under oil immersion seen to be punctate to finely echinulate, the echinulations often quite noticeable on the lighter-colored sides, chiefly 5-7μ in diameter. Fig. 35.

On Gramineae:

Sorghum vulgare Pers. Washington, Oregon
Sorghum vulgare var. *sudanense* (Piper) Hitchc. Washington
Sorghum vulgare var. *technicum* (Koern.) Jav. Washington

Fig. 35. Kernel smut of sorghum, *Sphacelotheca sorghi*: A. Habit, on *Sorghum vulgare technicum* (Broom corn). B. Spores, x approx. 800.

Spore germination on nutrient media, at room temperature, usually begins in 18-24 hours, forming a 3- to 4-celled promycelium which buds off numerous sporidia from each cell.

37. USTILAGO VUIJCKII Oud. and Beijer. Oudemans Versl. Amst. IV. 3: 55. 1895.

Sori contained in the capsules and maintaining the form of the 3 ovules, naked, straw yellow, indurate; spores globose or subglobose to ovoid, mostly hyaline or pale yellowish but with darker spores (golden yellow to yellowish-brown) intermixed, deeply and strikingly reticulate, so as to appear spiny at the circumference, 13-21μ in diameter. Fig. 36.

On Juncaceae:

Luzula glabrata (Hoppe) Desv. Washington

The type of sorus and the reticulate spores exhibited by this smut strongly suggests it as a species of *Tilletia*. Observations of germinating spores, however, (in Europe) have definitely proved the fungus to belong to *Ustilago*.

Fig. 36. *Ustilago vuijckii*: Spores, x approx. 800.

38. USTILAGO ALSINEAE Clint. and Zundel North Amer. Flora 7(14): 991. 1939.

Sori in the capsules, surrounding the remains of the individual ovules, apparently naked within the capsule, dark brownish-purple, inconspicuous; spores globose, subglobose, to ovoid, deep brownish-purple, rather minutely reticulate, 10-14μ in diameter. Fig. 37.

On Caryophyllaceae:

Stellaria nitens Nutt. Washington, Idaho

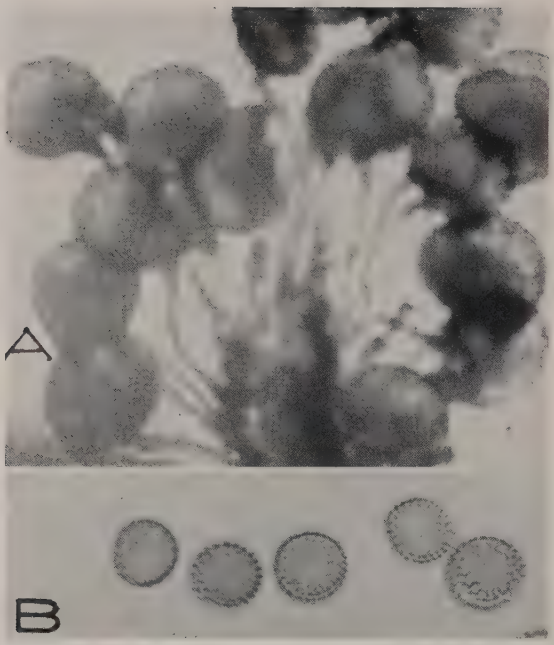

Fig. 37. *Ustilago alsinae*: A. Parasitized ovules of *Stellaria nitens*. B. Spores, x approx. 800.

39. USTILAGO VINOSA (Berk.) Tul. Ann. Sci. Nat. III. 7: 96. 1847.

Sori in the flowers, destroying usually both ovaries and stamens, granular-powdery, light purplish-brown; spores globose to subglobose or ovate, hyaline to pale violaceous or with a yellowish tinge, thick-walled, distinctly reticulate (oil immersion), appearing coarsely spiny at circumference, 7-10μ in diameter. Fig. 38.

On Polygonaceae:

Oxyria digyna (L.) Hill Washington

40. USTILAGO VIOLACEA (Pers.) Roussel Flore du Calvados etc. p. 47. 1806.

Sori in the swollen anthers, inconspicuous, filling them with a purplish spore-mass, powdery; spores mostly globose to subglobose, occasionally ovoid, pale violaceous or yellowish to brownish-purple, distinctly reticulate (as seen under oil immersion), 5-8μ in diameter. Fig. 39.

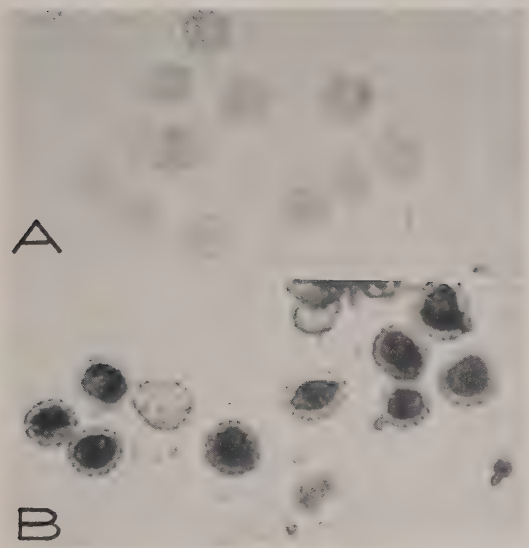

Fig. 38. *Ustilago vinosa*: Spores: A. surface view; B. median view (contents stained with cotton blue). A. and B. x approx. 1000.

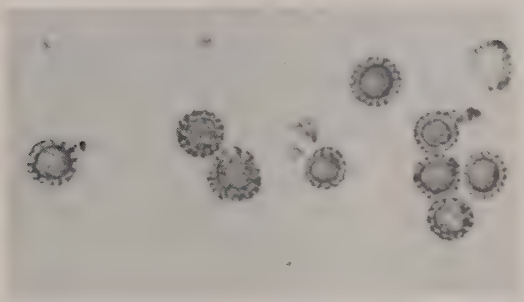

Fig. 39. *Ustilago violacea*: Spores, median view, x approx. 1000.

On Caryophyllaceae:

Arenaria lateriflora L. Washington
Silene multicaulis Nutt Washington
Silene oregana Wats. Washington
Silene watsoni B. L. Robinson Washington

This interesting smut represents one of the extremes in specialization to host tissues. It has even been reported that the presence of the smut fungus in a female plant of a dioecious host species causes the flowers to bear stamens, in the anthers of which the smut spores are borne, whereas normally of course the female flower would have no stamens.

In the taxonomic literature on smuts various authorities are given. Persoon is usually given credit for the specific name (as *Uredo violacea*) but different authors are credited with the transfer to the genus *Ustilago*. The combination given above is that given by Liro in Vol. I of his "Ustilagineen Finnlands" (see Bibliography) and seems to conform best to International Rules of Botanical Nomenclature.

Ustilago violacea is widespread over both hemispheres and on quite a variety of members of the *Caryophyllaceae*. Collections from these various hosts differ considerably in spore color and to a lesser extent in size and markings. This has provided good material for species-splitters but usually such split species are not morphologically distinguishable, because of intergrades. It seems much better to recognize only the one (admittedly composite) species.

41. USTILAGO CLAYTONIAE Shear Bull. Torrey Bot. Club 34: 317. 1907.

Sori within the ovary, formed from the ovules and surrounding their lenticular remains, purplish-black, somewhat indurate; spores

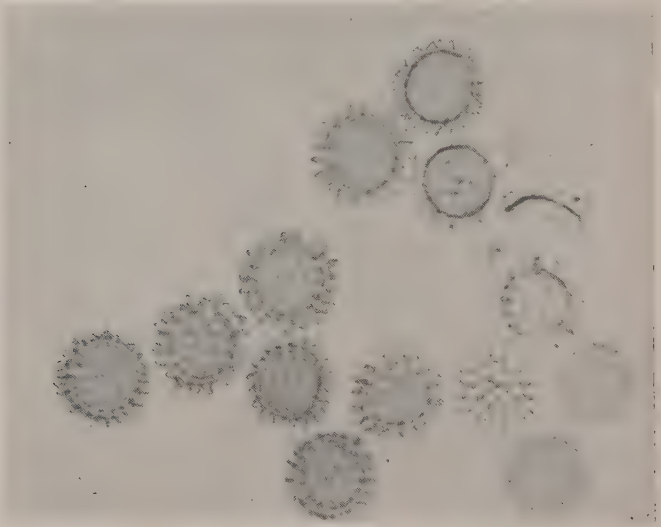

Fig. 40. Spring beauty smut, *Ustilago claytoniae*: Spores, x approx. 1000.

mostly globose to subglobose, occasionally ovate to elongate, deep violet, distinctly reticulate (with reticulations about 1-2μ in diameter and 1-1.5μ deep), 14-18μ in diameter. Fig. 40.

On Portulacaeae:

Claytonia linearis Dougl. Washington

This smut has not been reported from elsewhere in the entire world.

42. THECAPHORA DEFORMANS Dur. and Mont. Tulasne Ann. Sci. Nat. III. 7: 110. 1847.

Sori in the ovules, consuming most or all of them, forming a light reddish-brown, granular, spore-mass which is not evident until the more or less swollen pods are broken open; spore-balls mostly globose to subglobose, but also ovate to oblong, golden-brown to reddish-brown, composed of 5 to 20 or rarely more firmly-united spores, coarsely verrucose, 24-60 x 30-70μ; spores golden-brown to light reddish-brown, polyhedral from compression, coarsely verrucose on free surface, mostly 14-18μ in diameter. Fig. 41.

On Leguminosae:

Lotus micranthus Benth. Washington

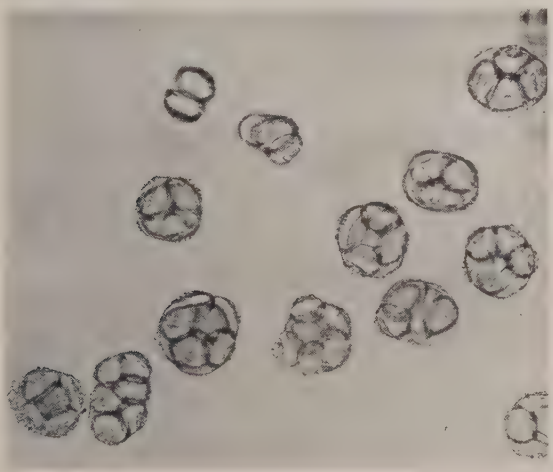

Fig. 41. *Thecaphora deformans*: Spore balls, x approx. 250.

43. THECAPHORA ATERRIMA Tul. Ann. Sci. Nat. III. 7: 110. 1847.

Sori at the base of the peryginia, bullate, rather well-concealed, granular-dusty, black; spore-balls globose, subglobose, to ovate or

oblong, opaque, dark olivaceous-brown, very firm, composed of 5-30 or more spores, 21-45 x 24-65μ; spores globose to polyhedral (especially from interior of spore ball), dark olive-brown, wall forming exterior of spore ball quite thick and more or less verrucose, mostly 10-14μ in diameter. Fig. 42.

On Cyperaceae:

Carex podocarpa R. Br. Washington

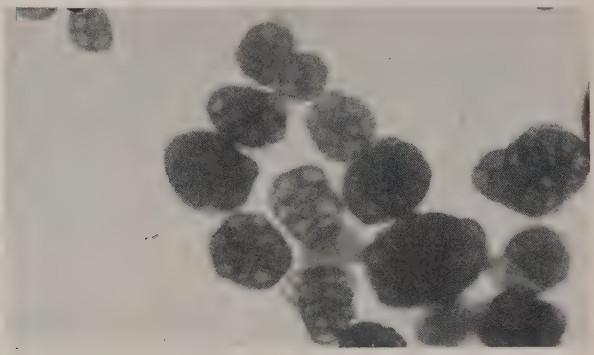

Fig. 42. *Thecaphora aterrima*: Spore balls, x approx. 250.

44. TILLETIA FOETIDA (Wallr.) Liro Maanviljelys. Talondellinen Koelaitos, Vuosikvija 1915-16, p. 27, 1920.

Tilletia levis Kuehn Rabenh. Fungi Europ. Cent. 17, No. 1697. 1873.

Sori in the ovaries, foetid, replacing the seeds and retaining their general shape, cylindrical, greenish-gray to brown, covered by the pericarp of the ovary; spores globose to ovoid or elongate, light grayish-brown to dark olivaceous-brown, smooth, chiefly 17-20μ in diameter or 17-20 x 18-22μ; sterile cells hyaline, thin-walled, smaller than the spores, mostly about 14μ in diameter. Fig. 43.

On Gramineae:

Triticum aestivum L. Washington, Oregon, Idaho

Spore germination is well understood. Usually after 3-5 days on water or water agar at 10-12° C. a hyaline germ tube emerges, curves upward, and bears at its apex a crown of long filiform sporidia, variable in number, usually 8-16, and which fuse in pairs while still attached to the promycelium.

Although rye and several other grasses [Goat grass (*Aegilops ventricosa* Tausch), crested wheat grass (*Agropyron cristatum* (L.) Beauv.), bearded wheatgrass (*A. subsecundum* (Link) Hitchc.), slender wheatgrass (*A. trachycaulum* (Link) Malte), English ryegrass (*Lolium perenne* L.),

and common ryegrass (*L. multiflorum* Lam.)] have been shown by inoculation to be susceptible to *Tilletia foetida,* in nature only wheat species and varieties have been found infected, except for one report of incidence on rye in Kansas.

The foetid odor (strongly reminiscent of a week-old emptied salmon can), especially noticeable in fresh collections, is due to the organic compound trimethylamine, and is responsible for the common name "stinking smut".

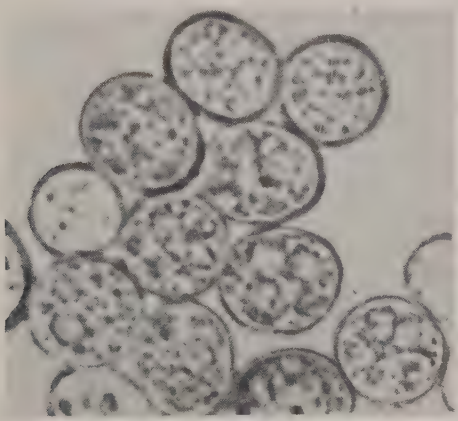

Fig. 43. Smooth spored stinking smut of wheat, *Tilletia foetida*: Spores, x approx. 800.

45. TILLETIA CARIES (DC.) Tul. Ann. Sci. Nat. III 7: 113. 1847.

Tilletia tritici (Bjerk.) Wint. in Rabenhorst's Krypt. Flora 1: 110. 1881.

Tilletia secalis (Cda.) Kuehn Deutsche Landw. Zeitung 19: 650. 1876 and Botanische Zeitung 34: 470. 1876.

Sori in the ovaries, foetid, replacing the seeds and having more or less their general shape (although frequently somewhat larger), usually some shade of brown due to the membrane (the pericarp of the ovary), spore-mass brownish-black; spores usually globose to subglobose, occasionally ovoid, light smoky-brown to dark reddish-brown, with reticulate epispore varying from minute shallow meshes, through large deep reticulations, to more or less cerebriform sculpturings, 15-23μ in diameter; sterile cells globose to subglobose, hyaline, usually smooth but sometimes faintly reticulate, thin walled, 12-18μ in diameter. Fig. 44.

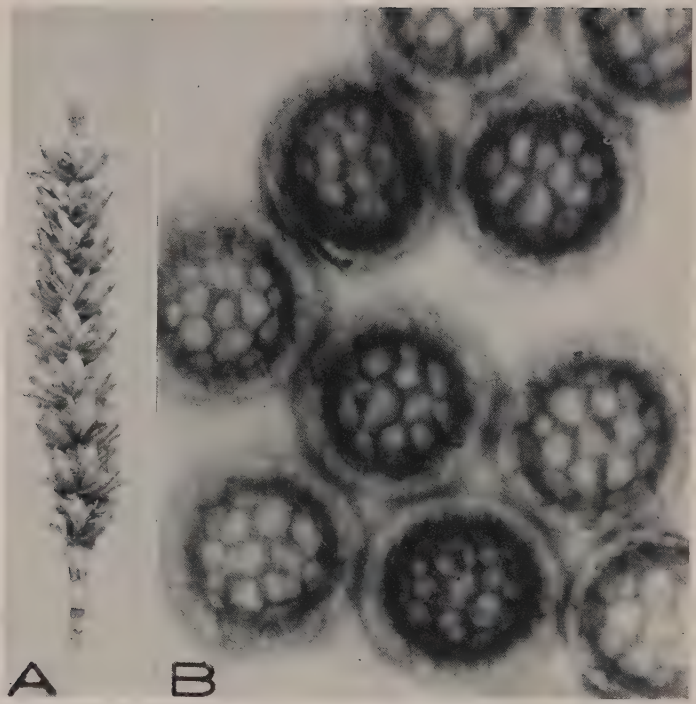

Fig. 44. Bunt, or stinking smut of wheat, *Tilletia caries*: A. Habit, on cultivated wheat. B. Spores, x approx. 1200.

On Gramineae:

Agropyron cristatum (L.) Gaertn. Washington
Secale cereale L. Washington, Oregon
Triticum aestivum L. Washington, Oregon, Idaho
Triticum dicoccum Schrank Washington
Triticum durum Desf. Washington
Triticum spelta L. Idaho

Spore germination is very similar to that of *Tilletia foetida.*

In addition to the hosts given above, inoculation experiments have proven the susceptibility of *Aegilops ventricosa, Agropyron subsecundum, A. trachycaulum,* and *Hordeum nodosum.*

In recent years a distinct strain of *Tilletia caries* (or it could be considered a separate species) has appeared in the Northwest which causes what is known as "dwarf bunt" or "short smut", due to the

extreme brevity of the culms of infected plants. This disease is not amenable to control by seed treatment and is increasingly becoming a menace to wheat production in this area. The smut balls or sori are nearly round in contrast to other strains of bunt or stinking smut, and they tend to be somewhat more solid in consistency. It is very difficult to induce the spores to germinate, it requiring several months pre-soak in water in the refrigerator and even then usually only a small percentage will germinate. The very high percentage of infection sometimes encountered in fields of wheat would indicate, however, that, in nature, spore germination is extensive.

46. TILLETIA GUYOTIANA Hariot Jour. de Bot. 14: 117. 1900.

Sori in the ovaries, slightly foetid when fresh, replacing the seeds, oval-cylindric, covered by the fragile, brown pericarp of the ovary, more or less concealed by the glumes, spore-mass light chestnut-brown, usually powdery-soft, but sometimes rather indurate; spores globose to subglobose or ovate, light golden-yellow to light chestnut-brown, adorned with beautiful, deep reticulations chiefly 21-24μ in diameter; sterile cells globose to ovate or polygonal, hyaline, smooth, thin-walled, 14-18μ in diameter. Fig. 45.

On GRAMINEAE:

Bromus brizaeformis Fisch. & Mey Washington, Idaho
Bromus japonicus Thunb. Washington
Bromus mollis L. Washington, Oregon, Idaho
Bromus racemosus L. Washington, Idaho

Spore germination has been observed only after the spores had been soaked for several weeks or more in water in the refrigerator at 2-3° C. A thick hyaline germ tube emerges, and frequently branches once. At the apex or apices there is borne a whorl of 8-12 long slender hyaline sporidia. Fig. 45, B.

47. TILLETIA FUSCA Ell. and Ev. Jour. Myc. 3: 55. 1887.

Sori in the ovaries, replacing the seeds, covered by the pericarp of the ovary which soon ruptures to expose the soft, powdery purple-brown to reddish-brown spore-mass; spores globose to subglobose, occasionally ovate or oblong, yellowish-brown to dark grayish-brown, strikingly reticulate (the reticulations deep and prominent and occasionally cerebriform), mostly 21-27μ in diameter; sterile cells globose to ovate or oblong, pale grayish-yellow, smooth and thin walled, 12-20μ in diameter. Fig. 46.

On GRAMINEAE:

Festuca dertonensis (All.) Aschers. & Graebn. Washington
Festuca microstachys Nutt. Washington
Festuca octoflora Walt. Washington, Oregon, Idaho
Festuca pacifica Piper Washington

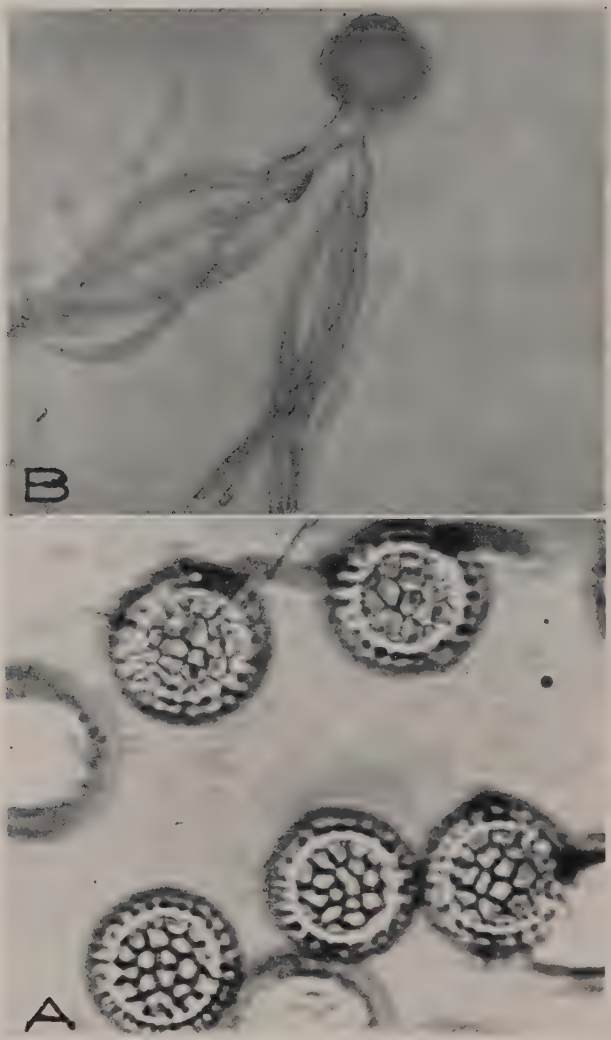

Fig. 45. Stinking smut of annual bromes, *Tilletia guyotiana*: A. Spores, x approx. 1000. B. Germinating spore, x approx. 800.

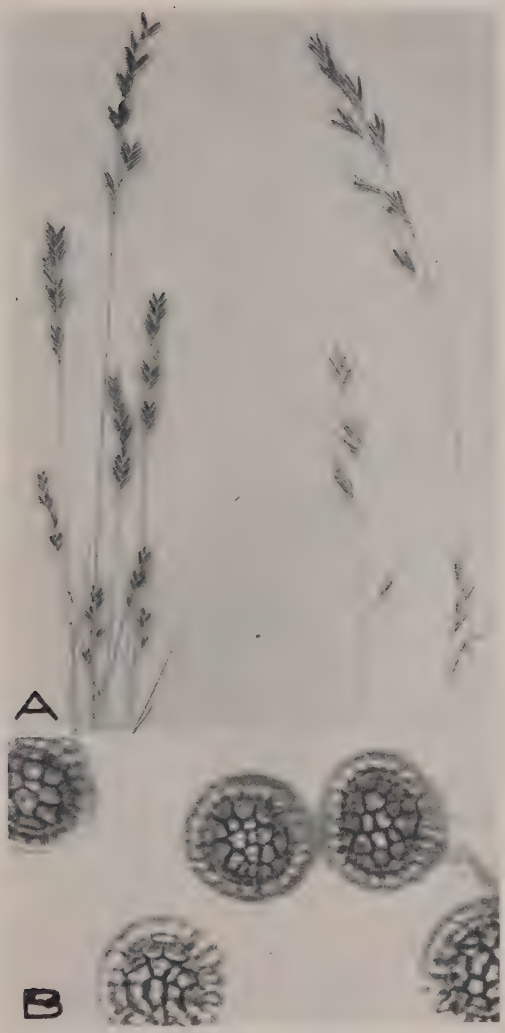

Fig. 46. Bunt of annual fescues, *Tilletia fusca*: A. Habit, on *Festuca octoflora* (left) and *F. pacifica;* B. Spores, x approx. 900.

Spore germination has been observed only after the spores had been soaked in water in the refrigerator for several weeks and then removed to a petri plate of water agar. A single unbranched promycelium emerges from the spore. If the promycelium is in contact with the agar surface it may elongate considerably before turning sharply into the air. If the promycelium arises into the air from the spore it is much shorter. In either case a whorl of 6-10 long slender primary sporidia is borne at the apex of the promycelium.

48. TILLETIA HOLCI (Westend.) Schroet. in Cohn. Beitr. 3. d. Pflanzen, 2. p. 365. 1877.

Sori in the ovaries, replacing the seeds, concealed by the glumes, covered by the pericarp of the ovary which upon pressure ruptures to expose the powdery brownish-black spore-mass; spores globose or subglobose, occasionally ovoid, yellowish-brown to olive-brown, deeply reticulate (with reticulations varying in size and even sometimes somewhat cerebriform), chiefly 21-28μ in diameter; sterile cells globose to somewhat angular, hyaline to pale smoky yellow, smooth, thin-walled, 17-24μ in diameter. Fig. 47.

On Gramineae:

Holcus lanatus L. Washington, Oregon

49. TILLETIA ELYMI Diet. and Holw. Bot. Gaz. 19: 305. 1894.

Sori in the ovaries, replacing the seeds, foetid when fresh, covered by the pericarp of the ovary, which upon rupture releases the powdery, reddish-brown to violaceous-brown spore-mass; spores chiefly globose or subglobose, light olive-brown to dark violaceous-brown, deeply reticulate (reticulations of variable size and shape, often cerebriform), 21-28μ in diameter; sterile cells globose or subglobose, hyaline to pale greenish yellow, smooth and thin-walled, 17-21μ in diameter. Fig. 48.

On Gramineae:

Elymus glaucus Buckl. Washington, Oregon

Spore germination has been observed only in spores soaked in water in the refrigerator for several weeks and then placed on a water agar plate at room temperature. The process of germination is very similar to that described for *Tilletia fusca.*

50. TILLETIA ASPERIFOLIA Ell. and Ev. Jour. Myc. 3:55. 1887.

Sori in the ovaries, minute, replacing the seeds, showing through the glumes as greenish-black, ovate bodies, covered by the remains of the ovary wall which upon rupture releases the brownish-black, dusty spore-mass; spores globose, subglobose, to ovoid or occasionally oblong, light yellowish-brown to dark olive-brown, enveloped by a thin

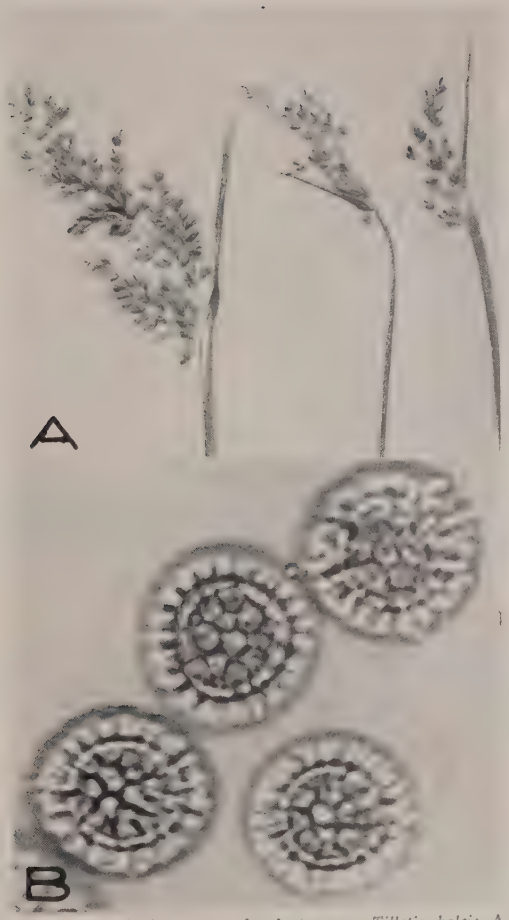

Fig. 47. Bunt or stinking smut of velvet grass, *Tilletia holci*: A. Habit, on velvet grass (*Holcus lanatus*). B. Spores.

hyaline membrane 1-1.5μ thick with a small hyaline apiculus often evident, distinctly reticulate to slightly cerebriform, chiefly 17-21μ in diameter, including the enveloping membrane; sterile cells mostly larger than the spores, hyaline to pale greenish, smooth, with thick distinctly laminated wall, globose to polygonal, 21-28μ in diameter. Fig. 49.

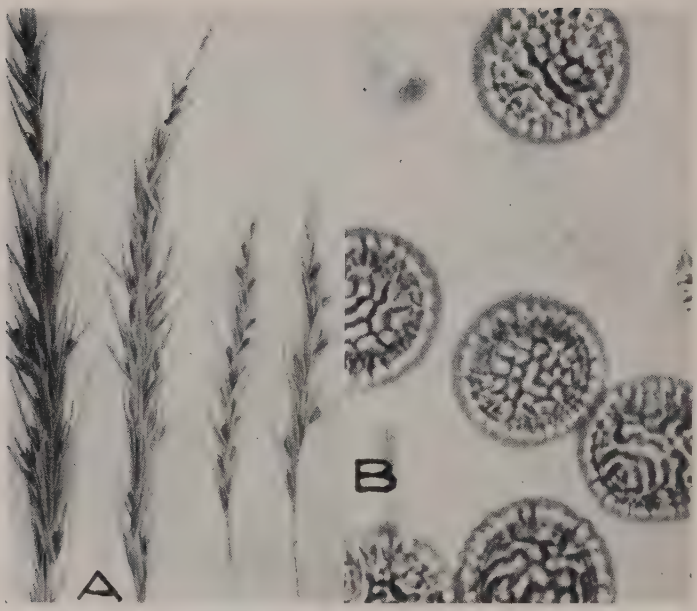

Fig. 48. Bunt or stinking smut of wild-rye, *Tilletia elymi*: A. Habit, on blue wild-rye, *Elymus glaucus*. B. Spores, x approx. 900.

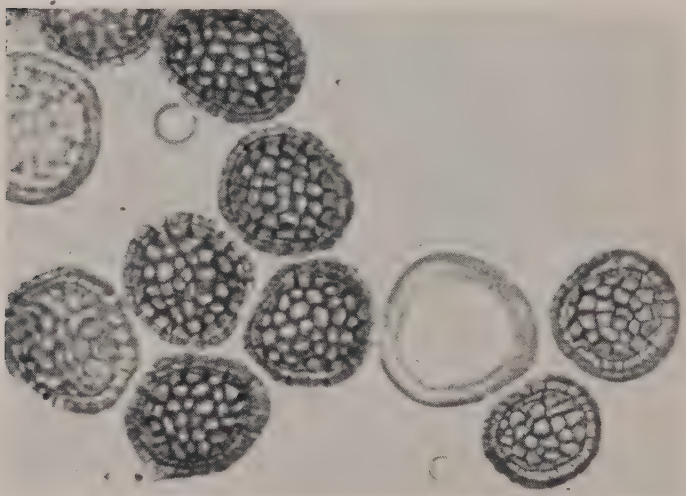

Fig. 49. Bunt of scratch grass *Tilletia asperifolia*: Spores, with one sterile cell, x approx. 1000.

On Gramineae:

Muhlenbergia asperifolia (Nees and Mey.) Parodi Washington, Oregon

51. TILLETIA CEREBRINA Ell. and Ev. Jour. Myc. 3: 56. 1887.

Tilletia airae Blytt Forh. Vid. Selsk. Christ. 1896: 31. 1896.

Sori in the ovaries, replacing the seeds, partially concealed by the glumes, covered by the remains of the ovary wall, which upon pressure ruptures to expose the dusty, brownish-black spore-mass; spores globose to subglobose or ovoid, light grayish-brown to olivaceous-brown, reticulate (with reticulations of varying size and shape, often cerebriform), chiefly 21-25μ in diameter; sterile cells globose or subglobose, hyaline to pale greenish-yellow, smooth, thin-walled, 12-17μ in diameter. Fig. 50.

On Gramineae:

Deschampsia caespitosa (L.) Beauv. Washington
Deschampsia danthonioides (Trin.) Munro Washington, Oregon
Deschampsia elongata (Hook.) Munro Idaho, Oregon

Spore germination has been obtained only after the spores had been soaked in water for 8 weeks in the refrigerator (2-3° C.) and then transferred to a plate of water agar. The process of germination is much as described for other species of *Tilletia*. At the apex of a simple, hyaline, sometimes septate promycelium there is borne a whorl of 8-12 long, filiform, primary sporidia.

Fig. 50. Bunt of hairgrass, *Tilletia cerebrina*: A. Habit, on annual hairgrass (*Deschampsia danthonioides*). B. Spores, x approx. 600.

PART FOUR

GALL-FORMING SMUTS

52. USTILAGO MAYDIS (DC.) Cda. Icones Fung. 5:3. 1842.

Ustilago zeae (Beckm.) Ung. Einfl. Bodens 211. 1836.

Sori on various parts of the host, evident as small to large and prominent galls, at first covered by a whitish membrane which upon rupture discloses the olive-brown, dusty spore-mass; spores mostly globose to subglobose, light olive-brown, rather prominently echinulate, chiefly 9-12μ in diameter. Fig. 51.

On Gramineae:

Zea mays L. Washington, Oregon, Idaho

Spore germination is characterized by the production of 4-celled promycelia, each cell producing sporidia.

This is the common smut of field, sweet, and popcorn. It is one of the most conspicuous smuts known, due to the familiar large galls which it produces on the corn plant. In some countries these galls are used as food when young.

53. USTILAGO CRUS-GALLI Tracy and Earle Bull. Torrey Bot. Club 22: 175. 1895.

Sori on the stems, nodes, leaves, and the inflorescence, prominent, globular or nodular, or as series of gall-like structures, quite variable in size, .5 mm to several centimeters in length, protected by a tough, hispid membrane of host tissue; spore-mass dusty, olive-brown; spores mostly globose to ovoid sometimes irregularly elongate, yellowish to olivaceous, rather prominently echinulate, 10-14μ in diameter. Fig. 52.

On Gramineae:

Echinochloa crus-galli (L.) Beauv.

Fig. 51. Common gall smut of corn, *Ustilago maydis*: A. Habit, on common field corn. Stalk gall on left; tassel galls on right. B. Spores, x approx. 900.

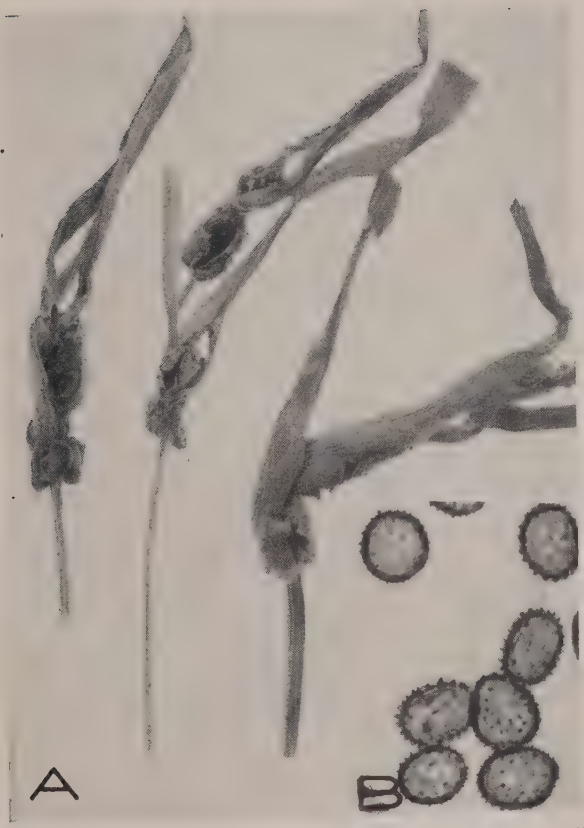

Fig. 52. Gall smut, *Ustilago crus-galli*: A. Habit, on barnyard grass, (*Echinochloa crus-galli*). B. Spores, x approx. 800.

Agropyron caninum
25.[3] Ustilago bullata
26. Ustilago hordei
3. Ustilago spegazzinii

Agropyron cristatum
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis
1. Ustilago aculeata
25. Ustilago bullata
26. Ustilago hordei
45. Tilletia caries

Agropyron dasystachyum
3. Ustilago spegazzinii
25. Ustilago bullata

Agropyron elongatum
3. Ustilago spegazzinii var. agrestis

Agropyron inerme
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis
6. Ustilago striiformis
7. Ustilago aculeata
25. Ustilago bullata

Agropyron intermedium
3. Ustilago spegazzinii var agrestis

Agropyron orientale var. lasianthum
25. Ustilago bullata

Agropyron pendulina
3. Ustilago spegazzinii var. agrestis

Agropyron repens
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis

Agropyron semicostatum
3. Ustilago spegazzinii

Agropyron sibiricum
3. Ustilago spegazzinii
19. Ustilago nuda

Agropyron smithii
3. Ustilago spegazzinii var. agrestis

Agropyron spicatum
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis
6. Ustilago striiformis
7. Ustilago aculeata
10. Urocystis agropyri
25. Ustilago bullata

Agroypron striatum
6. Ustilago striiformis

Agropyron subsecundum
6. Ustilago striiformis
25. Ustilago bullata

Agropyron trachycaulum
3. Ustilago spegazzinii var. agrestis
6. Ustilago striiformis
10. Urocystis agropyri
25. Ustilago bullata

Agropyron trichophorum
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis

Agrostis alba
6. Ustilago striiformis

Agrostis castellana
6. Ustilago striiformis

Agrostis exarata
6. Ustilago striiformis

Agrostis palustris
6. Ustilago striiformis

Agrostis stolonifera
6. Ustilago striiformis

Agrostis tenuis
6. Ustilago striiformis

Alisma plantago-aquatica
17. Doassansia alismatis

Arenaria lateriflora
40. Ustilago violacea

Arnica cordifolia
13. Entyloma arnicale

Arnica latifolia
13. Entyloma arnicale

Arnica mollis
13. Entyloma arnicale

Arnica spp.
13. Entyloma arnicale

Arrhenatherum elatius
24. Ustilago avenae

Avena byzantina
24. Ustilago avenae
26. Ustilago hordei

Avena fatua
24. Ustilago avenae
26. Ustilago hordei

Avena sativa
24. Ustilago avenae
26. Ustilago hordei

Barley (see *Hordeum vulgare*)

Beckmania syzigachne
6. Ustilago striiformis

Bentgrass (see *Agrostis*)

Blue-bunch wheatgrass (see *Agropyron spicatum, A. inerme*)

Blue wild-rye (see *Elymus glaucus*)

Bluegrass (see *Poa* species)

Broomcorn (see *Sorghum vulgare technicus*)

Bromegrass (see *Bromus inermis*)

Bromus anomalus
25. Ustilago bullata

Bromus brizaeformis
25. Ustilago bullata
46. Tilletia guyotinana

Bromus carinatus
10. Urocystis agropyri
25. Ustilago bullata

[3] The number refers to order of presentation in the text.

Bromus catharticus
25. Ustilago bullata
Bromus ciliatus
25. Ustilago bullata
Bromus commutatus
25. Ustilago bullata
Bromus erectus
25. Ustilago bullata
Bromus inermis
25. Ustilago bullata
Bromus japonicus
25. Ustilago bullata
46. Tilletia guyotiana
Bromus marginatus
25. Ustilago bullata
Bromus mollis
25. Ustilago bullata
46. Tilletia guyotiana
Bromus purgans
25. Ustilago bullata
Bromus squarrosus
25. Ustilago bullata
Bromus racemosus
25. Ustilago bullata
46. Tilletia guyotiana
Bromus rigidus
25. Ustilago bullata
Bromus secalinus
25. Ustilago bullata
Bromus secalinus var. velutinus
25. Ustilago bullata
Bromus sibiricus
25. Ustilago bullata
Bromus sterilis
25. Ustilago bullata
Bromus tectorum
25. Ustilago bullata
Bromus tomentellus
25. Ustilago bullata
Bromus vulgaris
25. Ustilago bullata
Buttercup (see *Ranunculus* species)

Calamagrostis canadensis
10. Urocystis agropyri
Canada wild-rye (see *Elymus canadensis*)
Carex aquatilis
27. Cintractia caricis
Carex douglassii
27. Cintractia caricis
Carex geyeri
27. Cintractia caricis
Carex podocarpa
27. Cintractia caricis
43. Thecaphora aterrima
Carex rostrata
28. Farysia olivacea
Catch-fly (see *Silene* species)
Cenchrus pauciflorus
34. Sorosporium syntherismae

Cheat (see *Bromus secalinus*)
Cheat grass (see *Bromus tectorum*)
Chickweed (see *Stellaria nitens*)
Claytonia linearis
41. Ustilago claytoniae
Colonial Bent (see *Agrostis tenuis*)
Corn (see *Zea mays*)
Crested wheatgrass (see *Agropyron cristatum*)

Danthonia californica
21. Ustilago residua
Deschampsia caespitosa
51. Tilletia cerebrina
Deschampsia danthonioides
51. Tilletia cerebrina
Deschampsia elongata
51. Tilletia cerebrina
Distichlis spp.
2. Ustilago halophila
Durum (see *Triticum durum*)

Echinochloa crus-galli
53. Ustilago crus-galli
Elymus angustus
3. Ustilago spegazzinii
Elymus canadensis
3. Ustilago spegazzinii var. agrestis
6. Ustilago striiformis
7. Ustilago aculeata
25. Ustilago bullata
26. Ustilago hordei
Elymus condensatus
3. Ustilago spegazzinii var. agrestis
Elymus dahuricus
3. Ustilago spegazzinii var. agrestis
Elymus excelsus
3. Ustilago spegazzinii
25. Ustilago bullata
Elymus glaucus
3. Ustilago spegazzinii
6. Ustilago striiformis
10. Urocystis agropyri
25. Ustilago bullata
26. Ustilago hordei
49. Tilletia elymi
Elymus junceus
25. Ustilago bullata
Elymus mollis
10. Urocystis agropyri
Elymus sibericus
6. Ustilago striiformis
25. Ustilago bullata
Emmer (see *Triticum dicoccum*)
Erigeron elatus
14. Entyloma compositarum
Erigeron salsuginosus
14. Entyloma compositarum

Fescue (see *Festuca species*)
Festuca dertonensis
23. Ustilago mulfordiana
47 Tilletia fusca

Festuca idahoensis
25. Ustilago bullata
Festuca microstachys
23. Ustilago mulfordiana
47. Tilletia fusca
Festuca octoflora
23. Ustilago mulfordiana
47. Tilletia fusca
Festuca pacifica
23. Ustilago mulfordiana
47. Tilletia fusca
Festuca reflexa
23. Ustilago mulfordiana
Foxtail grass (see *Setaria lutescens*)

Geum triflorum var. ciliatum
16. Whetzelia waldsteiniae
Giant wild-rye (see *Elymus condensatus*)
Glyceria elata
5. Ustilago longissima
Glyceria grandis
5. Ustilago longissima

Hairgrass (see *Deschampsia* species)
Holcus lanatus
6. Ustilago striiformis
48. Tilletia holci
Hordeum jubatum
10. Urocystis agropyri
20. Ustilago sitanii
25. Ustilago bullata
Hordeum jubatum var. caespitosum
20. Ustilago sitanii
Hordeum nodosum
10. Urocystis agropyri
20. Ustilago sitanii
25. Ustilago bullata
Hordeum vulgare
19. Ustilago tritici
26. Ustilago hordei

Idaho fescue (see *Festuca idahoensis*)
Indian rice grass (see *Oryzopsis hymenoides*)

Junegrass (see *Koeleria cristata*)

Koeleria cristata
10. Urocystis agropyri

Lolium perenne
6. Ustilago striiformis
Lotus micranthus
42. Thecaphora deformans
Luzula glabrata
37. Ustilago vuijckii

Madia sp.
14. Entyloma compositarum
Mannagrass (see *Glyceria* species)
Melica harfordii
3. Ustilago spegazzinii
Millett (see *Panicum mileaceum*)
Mountain brome (see *Bromus marginatus*)
Mountain daisy (see *Erigeron salsuginosus*)

Muhlenbergia asperifolia
50. Tilletia asperifolia

Oats (see *Avena sativa*)
Oniongrass (sse *Melica*)
Oryzopsis hymenoides
1. Ustilago nummularia
Oxyria digyna
39. Ustilago vinosa

Panicum dichotomiflorum
34. Sorosporium syntherismae
Panicum miliaceum
32. Sphacelotheca destruens
Phalaris arundinacea
8. Ustilago echinata
3. Ustilago spegazzinii var. agrestis
Phleum pratense
6. Ustilago striiformis
3. Ustilago spegazzinii var. agrestis
Poa ampla
3. Ustilago spegazzinii var. agrestis
Poa annua
11. Entyloma irregulare
Poa canbyi
6. Ustilago striiformis
Poa compressa
11. Entyloma irregulare
Poa juncifolia
11. Entyloma irregulare
3. Ustilago spegazzinii var. agrestis
Poa nevadensis
3. Ustilago spegazzinii
3. Ustilago spegazzinii var. agrestis
Poa palustris
3. Ustilago spegazzinii
Poa pratensis
11. Entyloma irregulare
10. Urocystis agropyri
6. Ustilago striiformis
Poa secunda
10. Urocystis agropyri
Poa vaseyochloa
11. Entyloma irregulare
Polygonum alpinum
30. Ustilago punctata
Polygonum bistortoides
9. Ustilago bistortarum
31. Sphacelotheca hydropiperis
Polygonum hydropiperoides
31. Sphacelotheca hydropiperis
Polygonum newberryi
30. Ustilago punctata
Polygonum persicaria
29. Ustilago utriculosa
Pond weed (see *Potamogeton*)
Potamogeton sp.
18. Doassansia martianoffiana
Puccinellia distans
3. Ustilago spegazzinii

Quackgrass (see *Agropyron repens*)

Quincy grass (see *Oryzopsis hymenoides*)

Ranunculus bongardi
12. Entyloma ranunculi
Ranunculus macounii var. oreganus
12. Entyloma ranunculi
Ranunculus sceleratus var. multifidus
12. Entyloma ranunculi
Rattlesnake grass (see *Bromus brizaeformis*)
Redtop (see *Agrostis alba*)
Rescue grass (see *Bromus catharticus*)
Ripgut grass (see *Bromus rigidus*)
Rye (see *Secale cereale*)
Ryegrass (see *Lolium perenne*)

Saltgrass (see *Distichlis*)
Sandbur (see *Cenchrus pauciflorus*)
Scratchgrass (see *Muhlenbergia asperifolia*)
Secale cereale
45. Tilletia caries
Setaria lutescens
22. Ustilago neglecta
Silene multicaulis
40. Ustilago violaceae
Silene oregana
40. Ustilago violacea
Silene watsoni
40. Ustilago violaceae
Sitanion hanseni
20. Ustilago sitanii
Sitanion jubatum
3. Ustilago spegazzinii
6. Ustilago striiformis
10. Urocystis agropyri
20. Ustilago sitanii
Slender wheatgrass (see *Agropyron trachycaulum*)
Sloughgrass (see *Beckmania syzigachne*)
Smart weed (see *Polygonum species*)
Smooth brome (see *Bromus inermis*)
Sorghum (see *Sorghum vulgare*)
Sorghum vulgare
36. Sphacelotheca sorghi
Sorghum vulgare var. sudenense
36. Sphacelotheca sorghi
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Spring beauty (see *Claytonia linearis*)
Squirrel-tail (see *Hordeum jubatum, Sitanion jubatum*)
Stellaria nitens
38. Ustilago alsineae
Stipa comata
1. Ustilago nummularia
Streptopus roseus
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Tar weed (see *Madia*)
Timothy (see *Phleum pratense*)
Trientalis latifolia
15. Tuburcinia trientalis
Triticum aestivum
10. Urocystis agropyri
19. Ustilago nuda
44. Tilletia foetida
45. Tilletia caries
Triticum dicoccum
45. Tilletia caries
Triticum durum
45. Tilletia caries
Triticum speltum
19. Ustilago nuda
45. Tilletia caries

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Water plantain (see *Alisma plantago aquatica*)
Western wheatgrass (see *Agropyron smithii*)
Wild oats (sse *Avena fatua*)
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[4] The number refers to the order of presentation in the text. Names in italics are synonyms.

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[5] In the literature references given here an attempt has been made to include the major taxonomic treatises, those works on other phases of smut studies which are more or less compendia and which contain many more references for the student, and certain other works having a direct bearing on the nomenclature or other aspects of the smuts of Washington.

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